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PRESIDENTIAL ADDRESS

THE DEVELOPMENT OF SCIENTIFIC POLICY
IN SOUTH AFRICA

By S. M. Naudé

President, Council for Scientific and Industrial Research

(Read March 16, 1960)

A study of the development of scientific research in South Africa over the last sixty to seventy years reveals that research in different fields was organized in order to overcome problems of immediate practical importance which the country had to face. It would take me too long to trace the development in every single instance, but a brief discussion of a few examples should be both interesting and illuminating.

The Onderstepoort of today, which we all know as one of the world's leading laboratories in the field of veterinary science, owes its existence to the outbreak of rinderpest in South Africa in 1896. President Kruger invited Dr. Arnold Theiler to investigate whether the cattle disease in the northern parts of Transvaal was really rinderpest. Theiler set up a small temporary laboratory at Daspoort, north of Pretoria. Besides studying the riddle of rinderpest and suggesting counter-measures, he did excellent work on a number of South African animal diseases during the ensuing years. When the Transvaal was granted self-government in 1908, General Botha decided to set up a large veterinary research institute at Onderstepoort. This institute was opened on October 1, 1908.

The success of Onderstepoort no doubt prompted the governments of the four provinces before Union and the Union Government after 1910 to tackle research on all the various problems in different fields of agriculture very seriously. In due course five agricultural colleges were founded, viz. Cedara in Natal, Grootfontein at Middelburg as well as Elsenberg near Stellenbosch in the Cape, Glen near Bloemfontein in the Orange Free State and the Potchefstroom Agricultural College in the Transvaal. In addition, the Union Department of Agriculture developed several laboratories specializing in particular fields. This development culminated in the creation of Faculties of Agriculture at the Universities of Stellenbosch, Pretoria, Natal and the Orange Free State.

A similar development followed in the field of medical research as a result of the stream of Native labour coming to the Witwatersrand from various parts of southern and central Africa. In 1912 the South African Institute for Medical Research was established by agreement between the Witwatersrand Native Labour Association of the Chamber of Mines and the Union Government. It was established primarily to conduct researches and investigations into the prevention and treatment of human diseases, to elucidate the cause of diseases, to devise methods of diagnosis and to

pursue studies in the fields of pure and applied bacteriology, pathology, parasitology, pharmacology and other branches of medical and allied sciences.

Although primarily established for research, the Institute, which was the only laboratory of its type in the Transvaal, subsequently agreed to undertake public health, medico-legal, pathological, bacteriological, sociological, clinical and other routine investigations and to manufacture vaccines, sera and various other products and appliances. Work on problems of direct concern to the mining industry was also initiated, viz. silicosis and pneumonia which had become a serious problem among mine Native labourers.

In this way the staff of the Institute grew from 25 in 1917 to over 800 today. It now has 22 branches all over South Africa. On the routine side, about 9,000 investigations were done in 1914 and this figure has risen to $1\frac{1}{2}$ million done annually at present.

The Institute can pride itself on several notable medical discoveries. A trend is developing towards concentrated research activities in specialized fields and in many instances the resources of the Institute are combined with those of other bodies and agencies in tackling various problems, such as arthropod-borne virus diseases in conjunction with the Rockefeller Foundation, the Poliomyelitis Research Foundation and the Council for Scientific and Industrial Research; human biochemistry with the support of the C.S.I.R., and cardiovascular disease with the assistance of the Oppenheimer Foundation and the C.S.I.R. At present the Institute also accommodates the pathological section of the Pneumoconiosis Research Unit of the C.S.I.R., which is supported by the Chamber of Mines and the Mines Department of the Union Government.

In addition to these developments of research in the biological field, similar developments were taking place in the mineral field and many examples could be quoted to indicate the pattern which this *ad hoc* development assumed.

In short it can be said that from the earliest days of the Cape up to 1895, official interest in geological studies was very sporadic and short-lived and was aimed primarily at the investigation of mineral deposits rather than an understanding of the geological history of the land and the scientific search for minerals based upon such understanding. The year 1895 saw the birth of an officially recognized and continuing geological survey of the Cape of Good Hope which eventually developed into the Union Geological Survey with headquarters at Pretoria and this is now accepted as a vigorous organism essential to the well-being of the whole body politic.

From consideration of the development of research in the general geological field, we proceed to study the growth of the need for research in the specific field of coal, which is no doubt one of the richest assets we have in South Africa and on which our whole national welfare as a State rests very heavily.

It appears as if the need for fuel research as such was preceded by the occurrence of overheating and spontaneous combustion of South African coal loaded at Durban and Delagoa Bay in the period shortly after the termination of the First World War in 1919. This led to the inclusion in the Coal Act, No. 27 of 1922, of paragraph 3(3), which reads as follows: 'A Grading Committee may, in its discretion, refuse to issue

a grading certificate in respect of any coal submitted for grading if the liability of such coal to spontaneous combustion is deemed by the committee to constitute danger to life or property. The decision of the Grading Committee shall be subject to review by the Minister.'

Some sporadic investigations of coal were carried out in the period 1920–5 but the lack of reasonably comprehensive data was felt by many leaders of the coal industry and Government departments as well as by others engaged in planning for new industries, e.g. for the proposed iron and steel works and developments in the field of 'oil from coal'. An essential preliminary to the establishment of the iron and steel works was quite extensive pilot plant work on the production of coke from blends of Transvaal and Natal coals. Men such as Drs. P. N. Lategan and F. Meyer became increasingly interested in the establishment of a Fuel Research Institute where undivided attention might be given to the study of Fuel Research problems and where systematic survey work could be undertaken. In 1928 Dr. Meyer submitted a memorandum to the Government, in which a strong recommendation was made for the establishment of a Fuel Research Institute and this led to the drafting of the Fuel Research and Coal Act and the creation of the Fuel Research Institute in 1932.

So far, we have discussed the development of research facilities in four separate fields. In all four fields the development followed more or less the same pattern of an *ad hoc* approach. The first indication of a general approach to the question of research in South Africa appeared at the end of the First World War when the Research Grant Board was established in 1919 under the Union Education Department. This board was created mainly with the intention of fostering research in our universities. During the depression years of 1931–3, the funds available to the Board were almost completely provided by a small grant from the Carnegie Foundation.

This situation continued until 1945 when the Council for Scientific and Industrial Research was created to co-ordinate applied research in the physical and engineering fields. The Council was also entrusted with the duty of supporting research at the universities. During the fourteen years of its existence, the Council has built up extensive facilities for research in the fields of physics, chemistry, building science, mechanical engineering, personnel aptitudes and abilities, roads, water, telecommunication, nutrition, and, in 1956, took over responsibility for extensive facilities for standardization in industry.

The Council was also entrusted in 1947 with the responsibility of exploring and developing the whole field of medical research. This it has done, with the help and guidance of its Committee for Research in Medical Sciences by creating some twenty-one different medical research units at various medical faculties of universities and hospitals around scientists who had already shown their aptitude for research.

The C.S.I.R. has also had appreciable success in developing research in our universities. Whereas the total contribution by the Research Grant Board to university research was only £14,000 in 1946, the amount made available for 1960 to universities for non-medical projects amounted to over £120,000.

The present position of research in South Africa is that the C.S.I.R. is responsible to the Minister of Economic Affairs. The Fuel Research Institute is responsible to

the Department of Commerce and Industries. Agricultural research falls under the Department of Agricultural Technical Services. The Geological Survey and the Government Metallurgical Laboratory fall under the Department of Mines. The Atomic Energy Board, which is responsible for research in nuclear energy, is responsible to the Minister of Mines. Medical research in connexion with health problems falls under the Minister of Health. The Union Observatory, which covers research in astronomy, falls under the Department of Education, Arts and Science. Fisheries research is under the Department of Commerce and Industries; forest products research under the Department of Forestry; meteorology under the Department of Transport, and so on. On the whole, the picture of research organization in South Africa therefore represents a very uncoordinated pattern and experience over the last fourteen years has shown that this leads to a great deal of confusion and to frustration of the individual scientist, who constantly finds that he is entering the domain of some other department which has a first right to research in his field. This is the stage at which we should study the solutions found in other countries and should attempt to learn from their experience, which in most cases extends over a much longer period than ours in South Africa.

In Britain, the position up to 1959 was that, in the main, civil research was organized under four bodies, namely, the Department for Scientific and Industrial Research, the Agricultural Research Council, the Medical Research Council and the Nature Conservancy. These bodies were all responsible to the Lord President of the Council and under the direction of secretaries who were able to avoid overlapping in their functions.

Although this organization worked very well, Prime Minister Macmillan deemed it expedient, when he reshuffled his cabinet after the election in October 1959, to appoint a Minister for Science. In addition to the above bodies, the Atomic Energy Authority and the Overseas Research Council were placed under the same Minister. No Ministry of Science has been created and other Ministers retain executive responsibility for the scientific matters within their own departments. The Minister for Science is, however, responsible for broad questions of scientific policy outside the sphere of defence and is advised by the Advisory Council on Scientific Policy on general questions which relate to the whole field of civil science.

Statements made by Lord Hailsham, the first Minister for Science, make it clear that no attempt will be made to limit the freedom and initiative of universities or industry in determining the content of scientific education or the direction of research. He has stressed his anxiety to do nothing to interfere with the independence of Government-financed bodies. To quote from an article in *Nature* (October 24, 1959, Vol. 184-1, pp. 1255-8): '. . . he recognizes that if educational and scientific institutions are to function efficiently, they must retain complete integrity, and accordingly a high degree of independence.' As Lord Hailsham himself has said, 'Science in Great Britain increasingly touches life at every point. It is thus necessarily a partnership—and, since Britain is a democracy, it is a partnership in which everyone is invited to play a part. But the indispensable partners are industry, agriculture, medicine, teaching, the universities and Government—and, of course, both scientists

and non-scientists who play their part in the administration at the various branches of public and economic life. In all these spheres my task is to promote science. But only in part of one of these spheres of activity—that of Government—have I the power to achieve this by the use of authority as distinct from the use of encouragement, diplomacy, enthusiasm, example, precept or advice.'

Russia has perhaps advanced the furthest of all countries towards centralized control of all scientific effort. Ever since the time of Peter the Great, the Academy of Sciences played a leading role in Russia in all matters concerning education and scientific research. Today, in each of the sixteen republics of the U.S.S.R., there is an academy of sciences and these are co-ordinated by the Council for the Co-ordination of Research of the Academies of Sciences of the Soviet Union, founded in 1945. According to Prof. Dr. Karl Krüger (*Unser Wissen über die Sowjetunion*, Berlin, 1957), the number of scientific research institutes is most revealing. There were more than 2,800 research institutes in the Soviet Union in 1956. They are invariably well equipped with the most modern facilities. The number of persons exclusively engaged in scientific research (assistants excluded) at the close of 1956 was 239,400—according to figures published by the statistical services of the U.S.S.R. At the 6th Plenary Session of the Supreme Soviet in February 1957 the problems relating to scientific research and educational policy were discussed in great detail, with the result that 188·2 milliard roubles were voted for the educational institutes and for research in the financial year 1957—an increase of 24·5 milliard roubles over the previous year.

The important contrast with South Africa is that, to the Russians, scientific research is a vital question. The Russians have accepted that in the modern world national survival is a question of survival of the fittest and that the fittest nation is the nation which makes the best use of its brain power. In South Africa today, as the result of the haphazard development of scientific institutions, we have not the means of formulating, or even debating, a scientific policy, let alone the means for carrying it out. Nor can we even find out how much we, as a nation, are spending or should be spending, on scientific research.

In Russia, where all research is carried out and co-ordinated under Government auspices, it is interesting to note that there is much soul-searching, and apparently free discussion, on the best means of achieving co-ordination. Under the heading *Re-organization of the U.S.S.R. Academy of Science*, digests of articles which appeared in the newspaper *Izvestiya* (August 9, 1959) were published in the *LLU Translations Bulletin* (D.S.I.R. Lending Library Unit, December 1959, H.M.S.O., London). Academician Nikolai Semenov, a Nobel Prize winner, said that 'The Academy should on no account be turned into a kind of all-union ministry of science' and that, 'We must only, as Comrade N. S. Krushchev has pointed out, ruthlessly combat red-tape and indifference on the part of some of our people'. On personnel problems, he points out that 'one talented person can do ten times as much as a person who is mediocre and do it ten times better. . . . Certain leading scientists deliberately choose incapable assistants who can never become their rivals. Others look for "laboratory technicians" who will blindly obey them and they are not interested in having them put forward their own ideas and displaying initiative going beyond the limits

of the narrow task they have been set.' Academician Ivan Bardin, continuing the discussion, said that, 'Success in the work of the Academy of Sciences depends directly on the selection of personnel and not on this or that organizational structure. . . . The main trouble with the Academy of Sciences is that it turns research workers into office managers. Its institutes are becoming cluttered with unnecessary people who can only do routine work and are defending their positions by means of heaps of reprints of scientific papers that nobody needs.'

These reservations by eminent Russian scientists have a strange, familiar ring, and are sufficient warning of what can happen when science is controlled by bureaucratic administrators. Obviously organization, co-ordination and even apparently unlimited funds are not sufficient to produce first-class scientific research. Nevertheless, in the modern world, it is obviously necessary for nations to have a scientific policy—and the means to apply it.

In this respect, the United States of America is probably the most backward of all the leading countries of the world. And it is in the U.S.A. that there is the most urgent heart-searching. The new chairman of the Atomic Energy Commission of the U.S.A. is reported to have said recently that 'he is convinced that the United States—if it is not to become technologically and economically inferior to the U.S.S.R.—must work out methods of marshalling its scientific and technical talents for concentrated top priority work on projects of overriding significance'.

Referring to the above quotation attributed to Mr. McCone, Dr. Wallace R. Brode, the retiring president of the American Association for the Advancement of Science and scientific adviser to the Secretary of State, said on December 28, 1959: 'How can projects which are "overriding" and those which are of "lesser importance" be identified? Who is to make this allocation of relative effort? One of the most difficult tasks facing us is to achieve a long-range planning effort which would remove expediency as the sole controlling factor. A national science policy is needed for a wise and rational distribution of scientific activities, so that space, defence, education, atomic energy, oceanography, and medical research are not bidding against each other for limited available support. . . . Our problem today is that we have reached a saturation point with respect to available personnel. Hence, further expansion or support in many fields must of necessity require reduction of the active available material in other science programs.'

In 1959 a Federal Council for Science and Technology came into existence in the U.S.A. Dr. Brode is strongly in favour of a Department of Science for the U.S.A. and he sees it as this department's duty to determine the future policy of science in the United States. He says: 'The problems to be faced are these:

    (i) determination of the direction in which science will advance and of the areas in which continuing or new programs are to be supported;

   (ii) the emphasis and relative priorities to be placed on scientific programs, including not only the top-priority programs but also the minor programs which need to be kept alive and operating on a modest scale;

  (iii) the administration, financing, evaluation, and support of our science programs within the government; and

(iv) the distribution of responsibility for the carrying out of scientific programs between government laboratories and university, industrial, domestic and foreign facilities.'

A more definite move to develop a scientific policy in South Africa and to co-ordinate all our scientific efforts, was made when the Government, at the end of 1956, appointed the Advisory Council on Scientific Policy. This Council has since been studying our scientific activities and has made various recommendations to the Government in terms of a broad policy scheme. Before complete clarity can be obtained on the most suitable organization, several important matters will have to be carefully investigated. It is hoped that this Council will be able to convince the authorities of the importance, and indeed the indispensability, of a clear policy and a far more rational, effective organization than that which has developed, somewhat haphazardly, up to now.

The situation in South Africa was carefully analysed by Dr. Mönnig in his address to the South African Chemical Institute on May 5, 1959. He comes to the conclusion that scientific research in South Africa should be organized under four research councils.

He considers that the C.S.I.R. should retain the responsibility for the physical and engineering sciences including building research, road research, nuclear physics and telecommunications, as well as chemical and water research and personnel research. He thinks that metallurgical and fuel research should also be placed under the C.S.I.R.

He recommends that agricultural research should become the responsibility of a separate agricultural research council, and all biological research such as fisheries and forestry research and the research of museums and botanic gardens should also fall under the same council, for agricultural research is nothing but applied biology.

All medical research, including dental and veterinary research, should be placed under a medical research council.

The remaining group of subjects, viz. geology, geomagnetism, hydrology, meteorology and astronomy, might be placed under a fourth research council.

In the meantime, the Government has decided to make the Atomic Energy Board responsible for nuclear energy research and hence this Board should be considered as a fifth council controlling a specific field of research.

Dr. Mönnig proceeds to point out that a further necessary step is to bring all these groups together under a central authority. He feels that these councils or boards will not cause a lot of work to the central authority if they are all autonomous. It seems that the only possibility of getting such a central authority is either an authority under the Prime Minister or the appointment of a separate Minister of Science as in the United Kingdom. It is essential that the Advisory Council on Scientific Policy should fall under the same authority.

The advantages of such an organization would be manifold. In the first place, the heads of the various councils should get together frequently, but at least once a week, to discuss all new projects of research in their respective fields. In this way research going on in related fields could be co-ordinated and unnecessary overlapping

could be avoided. For the past five or more years, for example, the biochemists of the C.S.I.R. have been co-operating very fruitfully with the corresponding officers of the Onderstepoort Veterinary Laboratories on the problem of rumen digestion of animals. This type of co-operation should be the rule rather than the exception it is today.

Furthermore, the central authority would be able to see to it that policies relating to the application of salary scales will be the same in all five councils. It will also avoid the present competition for very scarce scientific staff between the various bodies and the available scientific personnel will be used in the best interests of the country. Certain services, such as information to the public and industry, translation from foreign languages and liaison with other countries could be largely pooled and centralized.

It will be obvious that, for such co-operation on the whole scientific front to be completely effective, all research bodies will have to be organized on the same basis, i.e. not some within and others outside the civil service.

With the help of the Advisory Council on Scientific Policy, the responsible authority will also be able to decide on the relative priorities of the various fields of research and funds and manpower could be directed accordingly.

A further advantage would be that recruitment of post-matriculation students by means of bursaries could be regulated in accordance with the needs of the various fields. The present system, under which a keen competition between the various bodies is taking place for the limited number of outstanding matriculants, will be avoided.

In this review, I have endeavoured to demonstrate that the present organization of science in South Africa is not satisfactory. I have also drawn attention to the dangers inherent in any scheme of organization which results in the control of research by bureaucratic administrators. This is a matter in which each country must work out its own salvation. Professional scientists, and professional bodies, must accept responsibility for bringing home to the general public, to legislators and to administrators that, in the modern world, scientific research plays an important part in public policies. In doing so, we could do worse than to accept the approach to the problem as defined by the Nobel Prize winning Russian Academician Nikolai Semenov: 'The history of the development of science from antiquity to our own day shows clearly that the main social function of science is to improve production, to increase the productivity of labour. To this should be added the treatment of the diseases of man, increasing his expectation of life. This does not mean, however, that science is an appendage to production. Its independent task is to make a profound study of nature, of the inner mechanism of natural phenomena, and consequently to harness the hidden forces of nature in the interests of man.'

These are universal truths, and the fact that they were enunciated in Moscow does demonstrate once again that a basic truth is as true in Moscow as it is in Washington or in Cape Town. This is taken for granted by scientists but does not always seem to be so obvious to administrators and to politicians.

It is to demonstrate this very point that, for a statement of the generally accepted principles which must be observed in any successful organization of scientific research,

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I have chosen the words of a Russian scientist. To round off the picture, I can do no better than quote a statement from the eminent British journal, *Nature*, on the conditions which are necessary for the successful application of these principles: 'The effective use of science and technology for the public welfare and in the affairs of State will not be ensured by establishing a Ministry of Science or appointing a special Minister. It will be secured in the measure, and only in that measure, in which Ministers and administrators, the Departments of State, the public corporations, industry and the public generally, are aware of the conditions and nature of scientific work, understand in some degree what science is doing and are prepared to provide the necessary support.' ('Organization of scientific and technological research in Britain', *Nature*, October 24, 1959, Vol. 184, pp. 1255–8.)
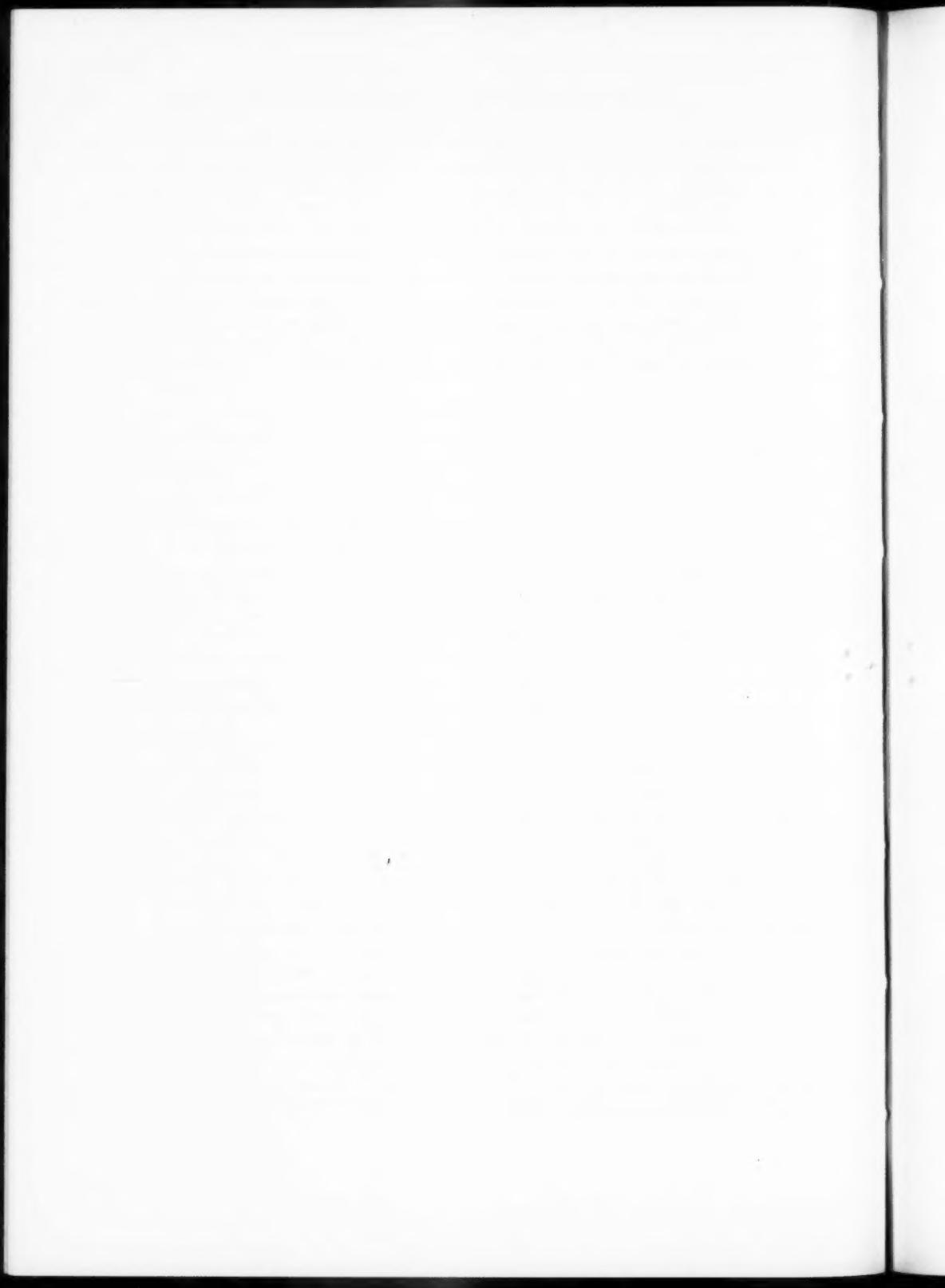
THE WATER AND HEAT RELATIONSHIPS OF FIDDLER CRABS (*Uca* spp.)

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(Communicated by J. H. Day)

The paper reports work on the water and heat relationships of five species of *Uca* at Inhaca Island, Moçambique. The species *urvillei, marionis, chlorophthalmus, annulipes* and *inversa* generally speaking occupy progressively more terrestrial habitats. They stand in this order (except *marionis*) as regards their sharply defined upper lethal temperatures (40·0 °C. for *urvillei*, 43·3 °C. for *inversa*) and in respect of transpiration rates (*inversa* being anomalous). Upper lethal temperatures are about 2 °C. lower for each species in September than in January. Lower lethal temperatures are less well defined and lie between 7·0° and 8·5 °C. for all species. No short-term acclimatization in crabs was found, although it occurs in *Oniscus asellus*. Measurements by fine thermocouples show that body temperatures are depressed by about 1·5° to 7·0 °C. in various conditions. Species which transpire faster generally have lower body temperatures. In direct sunlight the temperatures of living crabs are lower than those of dead, dry specimens, or that of the ground, and this permits crabs to live, in nature, in habitats which might otherwise be lethal. Eleven out of twelve *U. annulipes* survived for at least 11 days in 50% sea water, 7/12 survived in fresh water, and 3/12 in sea water. The results are discussed in relation to what is known about land isopods and other littoral crabs with reference to the general problem of the origins of a land fauna. The need for further information about environmental conditions and other matters is stressed.

CONTENTS

INTRODUCTION

The work now reported forms part of an investigation of the means by which littoral and terrestrial crabs are adapted to their habitats in respect of water, heat and salt requirements. Such information may be relevant to two more general fields of inquiry: the immediate factors which limit the distribution of species, and the problem of the origins of land faunas.

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There is already some information in this field (Pearse, 1950, and various authors in Waterman, 1960), but much of it concerns laboratory work and there is a lack of information about the responses of crabs to conditions in their natural environments. Verwey (1930) and Orr (1955) have investigated the temperature and humidity requirements of certain crabs, and Bliss (1956) measured these parameters in the habitats of *Gecarcinus lateralis* and other semi-terrestrial species. More recently Teal (1958, 1959) has published some useful information on environmental factors concerned in limiting the distribution of three species of *Uca* in Georgian salt marshes. There is also a good deal of information about thermal acclimatization in respect of metabolic rate (Vernberg, 1956, 1960; Roberts, 1957). But so far as I know there is only one paper (Vernberg and Tashian, 1959) on acclimatization in respect of lethal temperatures, and nothing on the actual body temperatures of any crabs.

The animals and their habitat

The work to be described was done during two short visits to Inhaca Island, opposite Lourenço Marques, in Portuguese East Africa (latitude 26° South, longitude 32° East) in September 1957 and January 1959.

It concerns five species of fiddler crabs, *Uca inversa* (Hoffman), *U. annulipes* (Milne-Edwards), *U. chlorophthalmus* (Milne-Edwards), *U. marionis* (Desmond) and *U. urvillei* (Milne-Edwards). These five species live in and around the mangrove swamps, and each has its favoured niche, though there is a certain amount of overlapping. In general, *U. inversa* lives in more open, sandy areas, where the mangrove bushes (*Avicennia marina*) are small and sparse. *U. annulipes* is probably the most common of all, and it lives in more sheltered and apparently rather wetter areas where the mangrove bushes are closer together. *U. chlorophthalmus* lives along the fringes of the thick mangrove area, in sandy mud. *U. marionis* and *U. urvillei* apparently prefer still wetter conditions, for *urvillei* lives in the dark mud lining channels through the mangrove swamps, and *marionis* occurs where these channels open out on to sand flats in soft, clayey mud. There is a good deal of size variation within each species, but in general they stand in the following order (from largest to smallest); *urvillei, marionis, inversa, annulipes* and *chlorophthalmus*. A large specimen of *urvillei* weighs about 15 g. while one of *chlorophthalmus* weighs about 3 g. All crabs in the following experiments were caught less than 24 hours previously and kept on moist sand.

Lethal temperatures

The first experiments were designed to establish the upper and lower limits of temperature tolerance in the five species. Preliminary observations showed that 5 °C. and 45 °C. were lethal for all crabs. Further preliminary work also showed that crabs immersed in water at these temperatures died in from 80 seconds to 4 minutes (the larger species taking the longer time).

Crabs were then immersed in cold or hot water and their temperatures were measured by means of thermocouples mounted in small hypodermic needles, to

find the speed of temperature equilibration between the body of the crab and the surrounding water. (A fuller description of the thermometric equipment is given on p. 77.) Starting with crabs at laboratory temperature (about 25 °C.) *annulipes* and *chlorophthalmus* attained equilibrium (within 0·2 °C. of the water temperature) within 1·5–2 minutes, while *inversa* took up to 4 minutes, and the larger *urvillei* and *marionis* took from 5 to 6 minutes.

In the definitive experiments, six crabs were used at a time. Each group was placed in a large thermos flask of water whose temperature was known to the nearest 0·1 °C., and left for 15 minutes. The temperature was then read again and the crabs
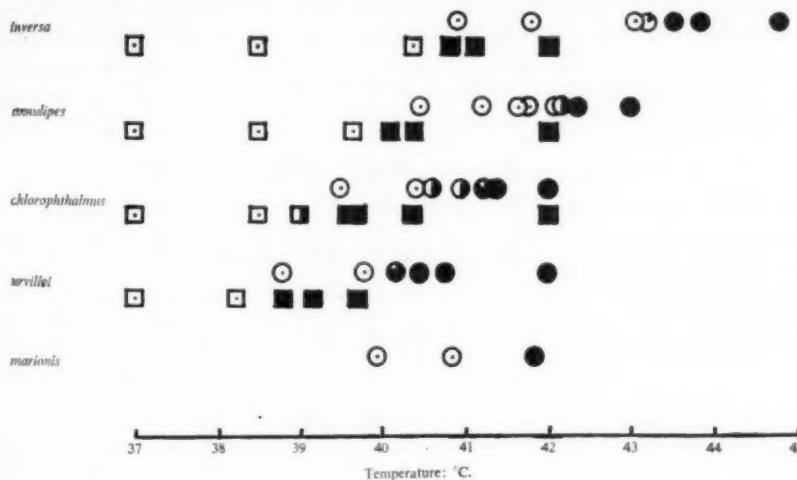

FIGURE 1

Upper lethal temperatures of five species of *Uca*. Each symbol represents the results for six crabs and the number of dead crabs is shown by shading the symbol proportionately. Circles refer to observations in January 1959; squares to those in September 1957. The species differ in respect of their upper lethal temperatures, and these are in each case about 2 °C. higher in January than in September.

were allowed to recover at laboratory temperature in air and were considered dead if they could not right themselves from an upside down position in 2 minutes. Only very occasionally did a crab which failed to right itself in 2 minutes subsequently recover. The final water temperature differed from the original by from 0·1° to 0·5 °C. largely because of the thermal capacity of the crabs. In expressing the results, the mean of the original and final temperatures has been used to represent the temperature during exposure. No crab was used for more than one exposure. So far as possible crabs of a similar size within any one species were used, although no difference could be found between large and small crabs as regards lethal temperatures when such differences were looked for.

The results obtained in January 1959 are shown in figures 1 and 2. It appears that at high temperatures the lethal level is reasonably sharp—it may be determined

to within about 0·5 °C. There is a clearly marked difference between the species as regards their upper lethal temperatures: that of *inversa* is highest, at about 43·3 °C., then follow *annulipes* (about 42·1 °C.), *chlorophthalmus* (about 40·8 °C.) and *urvillei* (about 40·0 °C.). *marionis* (for which there are only three determinations) shows a somewhat higher lethal temperature (about 41·4 °C.). So far as the first four species are concerned, the order in which they stand as regards lethal temperature corresponds well with what might be called for the time being their 'terrestrialness', but *marionis* is apparently aberrant.

A very different picture is presented by the results for the lower temperature limits (fig. 2). The lethal temperature is rather less clearly defined, and there is no demonstrable difference between the species. Above 8·5 °C. all the animals lived
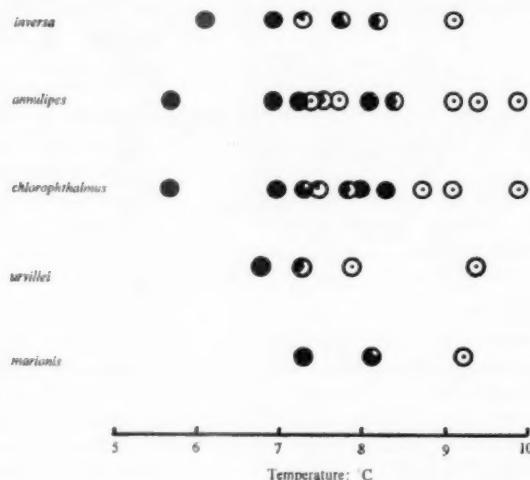
FIGURE 2

Lower lethal temperatures. Symbols as in figure 1. The species do not differ in respect of their lower lethal temperatures, and these are less well defined than are the upper limits.

and below 7·0 °C. they all died. The possible significance of these facts will be considered below (p. 85), after something has been said of the conditions to which the animals are exposed in nature.

ACCLIMATIZATION

(i) Acclimatization in *Uca* spp.

The results obtained in September 1957 refer only to the high lethal temperatures for four of the five species (fig. 1). Again there is a well-defined lethal level which varies from one species to another, and the species stand in the same order as before. However, there is an interesting difference in that the lethal levels are some 2 °C. lower in September 1957 than in January 1959. In September 1957 the mean daily

maximum and minimum temperatures at Inhaca were 27·0 °C. and 17·4 °C. respectively, while in January 1959 the corresponding figures were 29·2 °C. and 22·3 °C. Since this is so, and since a similar temperature difference occurs each year, the foregoing results suggest that acclimatization occurs in the summer and permits the crabs to live at a higher temperature than in the spring. No measurements were made of low temperature tolerance in September, so that it cannot be said whether or not acclimatization at the low end also occurs.

In view of this, it would be interesting to find whether acclimatization may also be brought about by exposure to high or low conditioning temperatures for short periods. In the limited time available a start was made on this problem, and crabs (*annulipes*) were kept for 18 hours either at 15 °C. or at 33 °C. (both approximate) and some of each group were then tested for their limits of heat and cold tolerance. No effect of the conditioning was found upon the temperature tolerance of these crabs, but the number of crabs used was too small to give a conclusive result.

(ii) Acclimatization in *Oniscus asellus*

Similar work was done by the writer in England some years ago on the land isopod, *Oniscus asellus* Linné, and it may be appropriate to report the results here.

For each experiment ten recently collected animals were used. Five of these were kept at a conditioning temperature (28° or 30 °C.) for 20 hours, before exposure for 1 hour in moist air (> 98% R.H.) to a given temperature in the vicinity of the lethal level. The other five were not so conditioned, but were exposed to the same near lethal temperatures at the same time.

TABLE I

Each entry represents the number of woodlice (*Oniscus asellus*) out of five which survived for 1 hour at the temperature indicated in the left hand column after the treatment indicated at the head of the remaining columns. A horizontal line is inserted at the temperature below which more than half the total number of individuals survived.

Temperature °C.	Unconditioned	Conditioned 20 hr. at 28 °C.	Conditioned 20 hr. at 30 °C.	Conditioned 4 hr. at 30 °C.
36·6	0		0	
36·4	0		1	
36·2	0	0		
36·0	0	3	0, 2	0, 0, 0
35·8	0	0	2	1, 0, 0
35·6	0, 0, 0, 0, 0	1	3	1, 1, 0, 0, 0
35·4	0, 0, 0		5	2, 1
35·2	0, 0, 0, 0	1, 1		3, 2
35·0	0, 0, 0, 0, 0	0, 4, 2	5	4, 3, 4
34·8	0, 1, 0, 0, 0	4, 4		3, 4, 4
34·6	1, 0, 0, 0	5		4, 4, 5
34·4	0			
34·2	0, 0, 0, 0, 1			5, 5, 4, 5
34·0	0, 0	5		4
33·8	2, 3, 3	5		
33·6	4	5		
33·4	5, 4	5		

The results are shown in table 1. The scatter is considerable, but if we consider the highest tolerable temperature to be that below which more than half the individuals survived, then it is clear that this is raised by 1·2 °C. from 33·8 °C. to 35 °C. by previous exposure to 28 °C., and by 1·8 °C. (to 35·6 °C.) by previous exposure to 30 °C., for 20 hours. Conditioning for only 4 hours was then attempted and a rather smaller effect was obtained. The lethal temperature was raised by 1·2 °C. after exposure to 30 °C. for 4 hours.

It may be concluded from these results that in the land isopod *Oniscus asellus* a rise in the upper lethal temperature occurs after the animals are subjected to conditioning temperatures for a few hours.

LOSS OF WEIGHT BY TRANSPIRATION OF WATER

Fiddler crabs spend a good deal of time on the surface of exposed mud and sand and this leads to loss of water by transpiration. Such water loss is, of course, a problem which confronts all terrestrial animals. It has the possible advantage of reducing the body temperature, but it may also lead to death by desiccation. One of the aims of the present work was to find out the extent to which transpiration occurs in *Uca* crabs and to assess its value, if any, to the animals in reducing their body temperatures.

The problem was approached first by measuring the rate at which water is lost by the animals in dry air. The results described below provide only a rough picture of what happens, because loss of weight was assumed to represent loss of
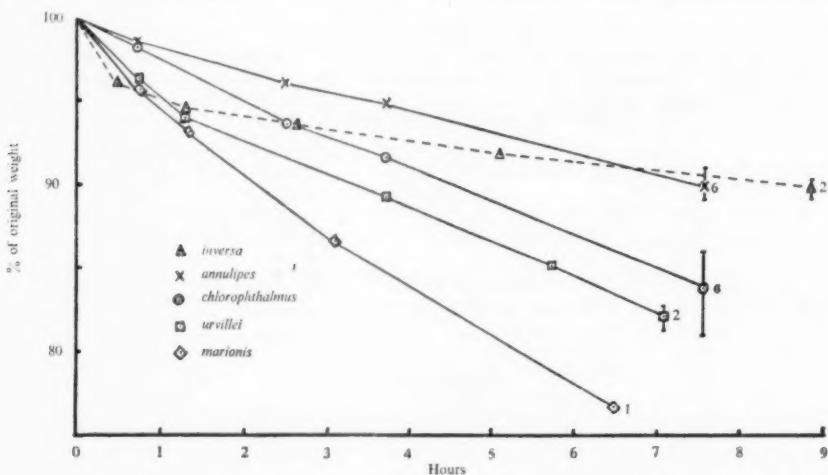

FIGURE 3

Loss of weight (presumed water) by five species of *Uca* in still dry air. Vertical lines through the last points indicate the range within each species and adjacent figures refer to the number of specimens used. *U. inversa* loses most rapidly for the first 30 minutes and then least rapidly.

water, and this may involve an error, though probably not a large one. Again, no information was obtained as to the site of water loss, which may have been from the gills, the general integument or particular regions of the integument.

Each crab was weighed separately to the nearest 0·005 g., suspended in a separate container in dry air over calcium chloride, and reweighed at intervals. The temperature was that of the laboratory, $25° \pm 2°C$.

The results are shown in figure 3, but they should be accepted with reserve because of the small numbers of each species used. The curves show the mean weights (as % of original weight) for each species, graphed against time. The vertical line through the last reading shows the range for each species at that time and the adjacent figures show the numbers of specimens used. Perhaps the least expected result is the rapid loss in weight which occurred in both specimens of *inversa* during the first half-hour. Apart from this the rates of loss are in keeping with the 'terrestrialness' of the species: *inversa* (after the first rapid drop) lost least rapidly, and was followed by *annulipes*, *chlorophthalmus*, *urvillei* and *marionis*, in that order. At the end of these exposures all the *chlorophthalmus* and the single specimen of *marionis* were dead; all the *inversa*, *annulipes* and *urvillei* were alive.

THE EFFECT OF TRANSPIRATION ON BODY TEMPERATURE

We may now consider the results of a series of experiments in which the effect of transpiration on body temperature was measured in a variety of conditions. In nature the body temperature of an animal is that temperature at which heat lost is just balanced by heat gained. Several factors are involved in this balance: thus heat is lost by evaporation of water, by convection to the surrounding medium, by conduction and by radiation; heat is gained by metabolism, by radiation, by convection and by conduction. Radiation, conduction and convection may work in either direction and may therefore lead either to a net gain or to a net loss of heat. A single physical factor in the environment may affect the balance in more than one way, thus the effect of wind speed may be felt through convection and through evaporation.

In nature, since many of the relevant factors fluctuate, the body temperature of a poikilotherm may be expected to vary, often rather widely and suddenly, so. that the analysis of the effect of each of the factors involved is extremely difficult and not very profitable. In the laboratory, however, it is possible to isolate at least some of the factors and to study their effects, so that we may then at least begin to understand the significance of body temperatures measured in the field, even though the prediction of such temperatures from a knowledge of physical conditions may remain impossible.

The present experiments on body temperature were done mostly in the laboratory, but a few readings in the field were also made. Temperatures were measured by copper-constantan thermocouples and a Doran minipotentiometer. For measuring body temperatures, the couples were made of 47 S.W.G. wires mounted in fine hypodermic needles. For air and ground temperatures, the couples were unmounted and made of 40 S.W.G. wires. With this equipment, temperatures could be read to

within ± o·1 °C. The cold junction of the thermo-electric circuit was at o °C. in ice and water unless otherwise stated.

In some of the following experiments the crabs were to be exposed to direct sunlight, and since this might lead to differences of body temperature in different parts of the body, a preliminary investigation of this possibility was made. Two crabs, one *inversa* and one *urvillei*, were exposed side by side with the sun to their right. Thermocouples were inserted into each crab in four places: (i) below the right dorso-lateral margin of the carapace, (ii) under the posterior margin of the carapace, but off centre to avoid the heart and central nervous system, (iii) in the left gill chamber, and (iv) below the frontal margin of the carapace near the base of the left eye stalk.

Two sets of readings were made after the temperatures had settled down and they both show (table 2) that in each position the temperature of *urvillei* was below that of *inversa*, which might be expected because the former transpires more rapidly; also the temperature in position (i), where the maximum effect of direct insolation was felt, was always higher than that in the other positions. In all further work the thermocouple measuring a crab's temperature was inserted in position (ii).

TABLE 2

Temperatures of different parts of the bodies of crabs when insolated from the right.

	Uca inversa		Uca urvillei	
	Air 31·1 °C.	Air 32·0 °C.	Air 31·1 °C.	Air 32·0 °C.
1. Below right dorso-lateral margin of carapace	37·9	39·8	36·0	38·7
2. Below posterior margin of carapace	37·2	38·7	34·6	36·0
3. In left gill chamber	35·6	37·2	34·4	34·8
4. Below frontal margin of carapace	37·2	39·6	35·8	37·9

(i) Laboratory experiments

The first experiment was designed to find the effect of evaporation into unsaturated air upon body temperature. Three species of crabs were used, *inversa*, *chlorophthalmus* and *urvillei*, and one specimen of each was kept in saturated air in a desiccator while the other was tethered by cotton on the laboratory bench. A thermocouple was inserted into each crab, and other couples measured the air temperature both inside the desiccator and above the bench. All the crabs were alive throughout the experiment. They were exposed for about 1 hour and temperatures were read every few minutes.

The results are shown in figure 4. After an initial settling-down period, the temperatures of the air inside and outside the desiccator and those of the three crabs

in saturated air, were all effectively the same. The temperature of the crabs in unsaturated air, however, were depressed by something like 1·5° to 2 °C. There was no clear correspondence between the amount of temperature depression and rates of transpiration in the three species, although it may be significant that the temperature depression shown by *inversa* was the greatest of the three during the first half-hour or so, and became the least thereafter, for this does correspond with the unexpectedly rapid loss of water for a short time found previously in *inversa* (p. 77).
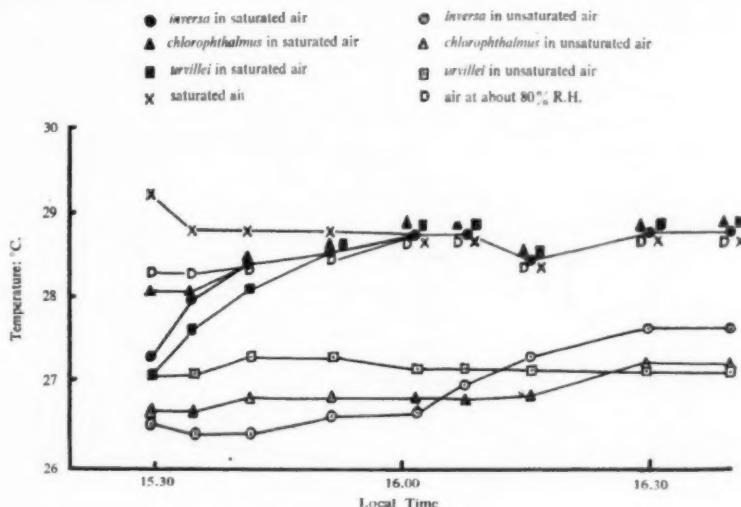
FIGURE 4

The body temperature of three species of *Uca* in saturated and unsaturated (about 80% R.H.) air. Temperatures of the crabs in unsaturated air are depressed by some 1·5°–2·0 °C. as a result of transpiration. *U. inversa* shows the greatest depression for the first 30 minutes or so, and then the least (compare fig. 3).

The relative humidity of the air in the laboratory was about 80% or above, so that evaporation was restricted. In the following experiment, the 'dry air' crabs were kept in a desiccator over calcium chloride, where the relative humidity was below 25%. *U. annulipes* and *urvillei* were used and the ambient temperature was approximately the same, but, as figure 5 shows, the temperature depressions were a good deal greater than in the previous experiment. *U. annulipes* showed a depression of rather more than 4 °C. and *urvillei* one of more than 6 °C. These depressions must, of course, be due to transpiration of water since they do not occur when the air is saturated with water vapour, and they correspond, so far as order is concerned, with the known rates of transpiration of the crabs. This experiment lasted for over 5 hours, at the end of which the crabs were still showing full temperature depressions.

(ii) Experiments in partially controlled conditions

The next step in this series of experiments was to expose individuals of various species to semi-natural conditions and to compare their temperatures with those of the immediate environment. At the same time, thoroughly dried dead crabs were exposed, so that by comparing their temperatures with those of the living crabs, an estimate could be made of the effect of transpiration alone upon temperature in the conditions of the exposure. Several such exposures were made on the open veranda of the laboratory at Inhaca, either in shade or in direct sunlight. Figure 6 shows the results of one such exposure made on January 10, 1959.
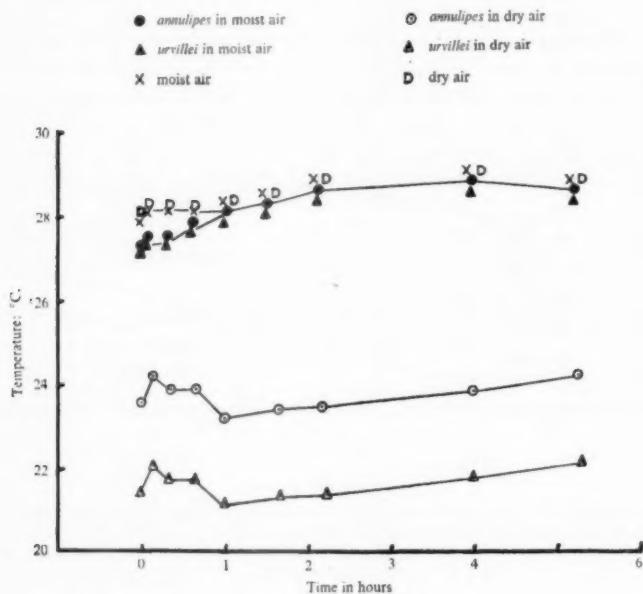
FIGURE 5

The body temperature of two species of *Uca* in saturated and dry air. Temperature depressions in dry air are greater than those shown in figure 4 because the rate of transpiration is higher. *U. urvillei* shows a greater depression than *annulipes*, and this reflects their respective transpiration rates.

In this experiment, both living and dried specimens of *inversa*, *annulipes* and *urvillei* were used. Ground and air temperatures were also taken and the ambient humidity varied between 72% at the beginning and 82% at the end of the experiment. In figure 6 the readings for *annulipes* are omitted for the sake of clarity. They are referred to, however, in the text.

The crabs were mounted upon a wooden board (the 'ground') by tethering them with cotton, and thermocouples were inserted. After this preparation which was done in the laboratory, the whole assembly was moved outside into direct

sunlight and readings were commenced. As figure 6 shows, all temperatures began
to rise rapidly, but after a few minutes they separated roughly into two groups:
a higher group (between 37.5° and 42°C.) comprising the ground temperature and
the temperatures of the dry crabs (including that of *annulipes* which is not shown in
the figure); and a lower group (between 31° and 35°C.) comprising the temperatures
of the living crabs (again including *annulipes*) and of the air 2 cm. above the ground.
At 1602 hours the sun was obscured for about 3 minutes by a thin cloud, and this was
reflected in a general fall in temperatures. Thereafter, temperatures recovered until,
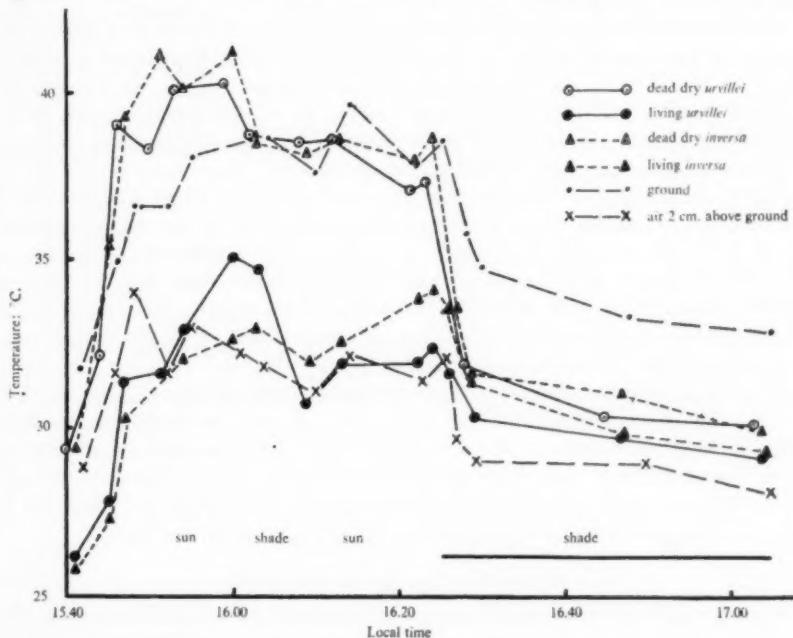
FIGURE 6

The temperature of living and of dead dry crabs in direct sunlight compared with ground and air
temperatures. For detailed comment, see the text.

at 1620 hours, the sun was obscured for the rest of the exposure, whereupon all
temperatures fell and remained between 28° and 30°C. with the exception of the
ground temperature, which remained higher.

The ground temperature, except during the first 13 minutes or so, was higher
than any other, and the air temperature was usually the lowest. The early slow rise
of the ground temperature as compared with the rapid rise of the dry crabs' tempera-
tures was probably due to the high thermal capacity of the 'ground'.

Many of the minor fluctuations in temperature may be accounted for by short
term changes in air velocity. Thus between 1546 and 1551 hours the temperature of a

dry *inversa* appears to rise, while that of a dry *urvillei* falls. But the temperature of *urvillei* was read at 1550, and that of *inversa* a minute later, and the low reading for *urvillei* may well be accounted for by a brief increase in air movement which, because the air was at that time several degrees cooler than the crabs, would have carried away heat by convection. This sort of occurrence underlines the fact that in nature poikilotherms do suffer quite large and rapid changes in body temperature. It also reminds us that the lines on the graph in figure 6 have no real meaning—they are simply reading devices which connect, in an arbitrary way, successive temperature measurements in one place.

For these sorts of reason, only a rather general picture of the state of affairs can be obtained from readings such as those in figure 6. Such information is indeed useful in its way, but, as mentioned above, we cannot expect to get very far with an analysis of the effects of the various factors involved by a detailed examination of the results of this sort of experiment. With this proviso, it is nevertheless interesting to see that from about 1605 hours onwards, *urvillei* had the lowest temperature of the three species of living crabs used, for this is in keeping with its known higher rate of transpiration. *U. annulipes* had the highest temperature among the living crabs for most of the time, although from 1610 (30 minutes after commencement) that of *inversa* rose to equal it. It is tempting to ascribe the comparatively low temperature of *inversa* (which is the most terrestrial in habitat) from 1550 to 1605 hours to an ability to transpire rapidly for the first 30 to 40 minutes, such an ability having been strongly suggested in two earlier experiments (pp. 77 and 79).

The results of other exposures were essentially similar to those just described, and need not be considered in detail here. Perhaps the most significant general conclusion that can be drawn is that living *Uca* crabs when insolated, even in rather high ambient humidities, have body temperatures some $5°$ to $8°C.$ below that which they would have but for transpiration. This may be of considerable significance if the ground temperature is at or above the upper lethal limit for the crabs.

(iii) Experiments in the natural habitat

We may now consider some measurements which were made in the natural habitat of fiddler crabs. These were all made on the afternoon of January 15, 1959, at low tide when the crabs and their habitats were exposed to direct sunlight. *Uca annulipes* was present in large numbers on a sandy area near the west bank of the 'Saco', between the outer edge of a mangrove forest and a footpath skirting the swamp. Measurements were made in three places within this habitat, along a line from the *Avicennia* mangrove forest to the footpath, and these are shown diagramatically in figure 7a.

Although the surface of the sand in some places was well above the lethal temperature of the crabs, the body temperatures of the latter were below lethal. However, one body temperature of $42·0°C.$ was measured and this is very near to the lethal temperature of *annulipes* for 15-minute exposures (fig. 1). There were many holes into which the crabs could retreat where the temperature was more equable. Air temperatures, measured 2 cm. above the ground, were much lower than ground

temperatures, so that no doubt the crabs' body temperatures were depressed partly by convection of heat to the air and partly by loss of heat as a result of transpiration. There was no danger of undue desiccation, for all the holes ran down to the water table and in some places shallow pools were adjacent.

It is interesting that greater numbers of crabs were present near the *Avicennia* trees and near the footpath (bordered by trees) than in the middle of the open area, even though temperatures were lower in the open. The temperatures of crabs in their holes were also measured, and found to be the same as the air temperatures
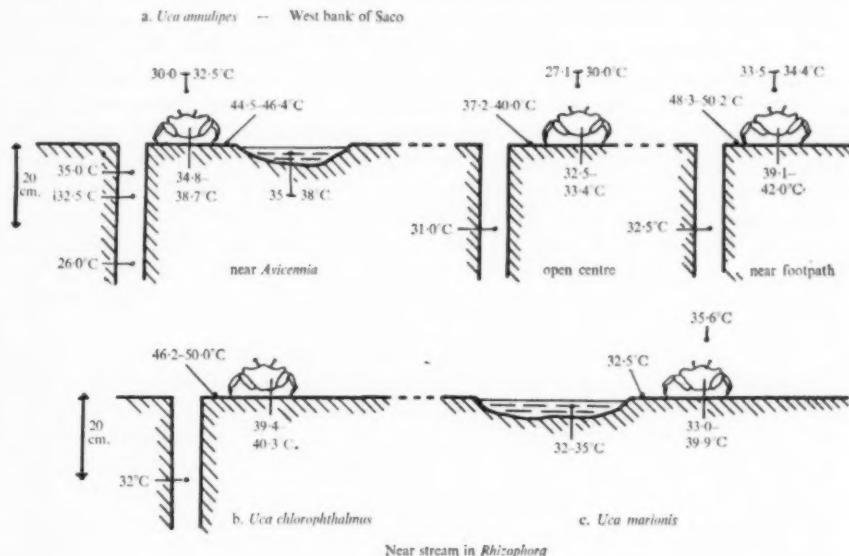
FIGURE 7

A diagrammatic representation of temperatures measured in the natural habitat of three species of *Uca*. The crabs' temperatures are usually below those of the ground, but even so they may be near the lethal level. Holes and pools form retreats for the crabs if their temperatures are too high or if they lose too much water. The scale shown refers to the holes only.

in the holes which are shown in figure 7a. Indeed, one crab, resting just inside a hole, was found to have a body temperature of 35 °C. (substantially equal to the air temperature in the same position), while another crab, just outside the hole, had a temperature of only 34 °C. even though it was in direct sunlight on hot ground. The crab in the hole could not have been losing heat by transpiration.

A few measurements were also made near a stream in the *Rhizophora* forest (where specimens of *chlorophthalmus* were present), and also where this stream debouched upon a wider channel in the habitat of *marionis*. These measurements are shown in figure 7b and c. *U. chlorophthalmus* was in one instance rather near its upper lethal temperature, but well below the local ground temperature, and again holes

were available for retreat. *U. marionis* (when the measurements were made at 1605 hours) was living on somewhat cooler ground, though the air temperature was higher than in the other two habitats.

SURVIVAL IN DIFFERENT SALINITIES

Jones (1941) and Gross (1955, 1957a, b, 1958) have studied *Uca crenulata* and *U. pugnax* in relation to osmotic problems and have found that these species regulate well in dilute and, to a lesser extent, in concentrated sea water. Teal (1958) also found that *minax*, *pugnax* and *pugilator* are capable of living in 15% sea water and higher concentrations for at least three weeks. Even in fresh water, more than half of the *minax* specimens lived for three weeks, although the other species died sooner.

It will be important in future work to study the osmotic problems which face species at Inhaca and to measure their osmotic tolerance and regulatory ability, as part of the general inquiry into their ecology. The following experiment was done as a simple approach to this side of the work. Specimens of *U. annulipes* were kept in dishes containing either sea water, fresh water or a 50% dilution of sea water, and in each case they were either provided with stones upon which they could climb out of the water, or compelled to remain submerged. The six dishes were kept in the laboratory. The water was changed once a day, and the temperature varied between 22 °C. and 26 °C. Six crabs were used in each dish.

Observations were made twice a day, when the position and activity of all the crabs were recorded. Most of the crabs were submerged most of the time and there was no significant difference between the groups in this respect. Neither was there any observed difference as regards activity. The results in an abbreviated form, showing deaths only and omitting days on which no change occurred, are shown in table 3. In sea water, 3 out of 12 were alive after 11 days; in 50% sea water 11/12 were alive; and in fresh water 7/12 were alive. In sea water, deaths occurred early if at all. In fresh water, the fewer deaths occurred rather later. The difference between survivals in 50% sea water and fresh water might occur once in four times by chance, that between survivals in 50% and 100% sea water is highly significant. The results suggest that 50% sea water is preferable osmotically to either sea or fresh water, and that the crabs possess either great osmotic tolerance or wide powers of regulation, or both. There was no evidence that continuous submergence is harmful.

TABLE 3

The number of crabs alive (out of six in each group) after periods of exposure to the salinities shown.

Days	Freshwater		50% sea water		Sea water	
	Stones	No stones	Stones	No stones	Stones	No stones
0	6	6	6	6	6	6
1	4	6	6	5	2	2
2–3	4	6	6	5	2	1
4–6	4	5	6	5	2	1
7–11	2	5	6	5	2	1

DISCUSSION

Judged by the degree of exposure to typically terrestrial conditions—unsaturated air, wind and direct sunlight—or by the period of time they are uncovered by tides, the species of *Uca* dealt with in the present work may with some confidence be arranged in the following order of decreasing landworthiness: *inversa, annulipes, chlorphthalmus, marionis* and *urvillei* (the order of the last two being doubtful). We may now ask whether the present results, which are largely physiological, help to explain the known distribution of the species concerned. It may be helpful also if the present results are compared with parallel information about the *Oniscoidea* (the only fully terrestrial crustacea) and about other littoral crustacea, so far as this is available.

(i) Lethal temperatures

As regards lethal temperatures, the results of the present work may be summarized as follows: there is a fairly sharply defined lethal temperature, which is different for the different species, and is higher in the summer than in the spring; whereas the lower limit is less well defined and is similar for all species. If, as seems likely from measurements made in the natural habitat, fiddler crabs are frequently exposed to conditions which in combination lead to body temperatures close to the upper lethal level, strong selective forces are likely to produce a rather homogeneous population with a temperature tolerance near the upper limit of what is physiologically possible for the species concerned. This may account for the sharp upper limits found. On the other hand, there is reason to suppose that the lower limit is not the result of strong selective pressures, since temperatures as low as $7-8\,°C.$ are seldom if ever encountered at sea level in tropical latitudes. A more heterogeneous population may therefore be expected in this respect, and this would account for the lack of sharpness in the lower limit. Furthermore, if there is no selective force tending to produce populations with the lowest possible temperature limits, each species is not, as it were, physiologically extended, and the low lethal temperatures may be determined by other factors which are the same for all species.

An elaboration of this hypothesis to account for acclimatization would be of little value until we know more about the causes of heat and cold death at the physico-chemical level.

So far as actual lethal levels are concerned, it seems that the most terrestrial species show the highest temperature tolerance—except that *marionis* is aberrant in showing a higher tolerance than might be expected. On the other hand, we still know very little about the range of conditions to which this species is subjected. Although it lives in moist areas, these are open and subject to direct insolation, probably to a greater extent than in the habitat of *urvillei*, and this might explain the relatively high temperature tolerance of *marionis*. Further measurements of temperature in the field are clearly desirable.

Verwey (1930) found that for two East Indian species of *Uca*, *signatus* and *consobrinus*, the highest near-lethal temperature in gradually rising temperatures was $42\,°C.$, and this is about the same as that for the common *Uca annulipes* in the

present work. Orr (1955) found that *Uca pugilator* dies after 30 minutes at 39 °C. and can live for up to 9 minutes even at 46 °C., which is a better performance than any found in the present experiments.

In contrast with the present results, Teal (1958) working with *Uca pagnax*, *U. minax* and *U. pugilator* from salt marshes, found that the upper lethal temperatures of all three species did not differ significantly, and lay between 39·5 ° and 40 °C. However, his crabs were half out of water, and exposed for 1 hour so that the conditions differ slightly from those in the present work.

As regards terrestrial isopods, *Armadillidium vulgare* (one of the most terrestrial crustaceans from temperate climates) survives at 42 °C. for 15 minutes. *Ligia oceanica* (one of the least terrestrial) dies after an exposure of 15 minutes to 34·5 °C. in saturated air (Edney, 1951); but this is a species from temperate climates, and Barnes (1936) found that *L. baudiniana* (a tropical species) survived for nearly an hour at 42 °C. This sort of comparison reminds us that it is quite illegitimate to compare a tropical with a temperate species and to draw conclusions as regards relative landworthiness. Upper lethal temperatures are just as likely to be related to latitude. It is however, safe to compare species in this respect if they all live at the same latitude.

(ii) Acclimatization

Although acclimatization in respect of oxygen uptake is well known in crabs (Roberts, 1957; Tashian, 1956; Vernberg, 1956, 1960; Demeusy, 1957), the only previous work on lethal temperature acclimatization is that of Vernberg and Tashian (1959), who compared tropical and temperate species of *Uca* in this respect and found that at 42 °C. or 44 °C. tropical species survived longer than temperate ones, unless both had been subjected to 15 °C. for 7 days, when the difference in survival at high temperatures disappeared. Temperate zone species, they found, were more cold resistant than tropical ones, and acclimatized to cold while tropical species did not.

The present work was concerned with a somewhat different question, for all the species were tropical, and survival or not for a fixed time at different temperatures was considered rather than time of survival at a fixed temperature. As a result, long-term acclimatization of about 2 °C. in the upper lethal temperature has been demonstrated in several *Uca* species, though attempts to find a short term effect have so far been inconclusive. The acclimatization here reported for the terrestrial isopod *Oniscus asellus* was the result of short period exposure and is not strictly comparable. However, the actual shift was similar, so that the fundamental mechanism may turn out to be the same.

The ability to acclimatize in respect of metabolic rate is probably of greater general significance, since it affects processes going on at all times, and permits animals to live economically yet actively at different latitudes and at different seasons. This type of acclimatization would be of great value in terrestrial conditions.

No advantage accrues to an animal as the result of ability to acclimatize in respect of lethal temperatures unless toleration of extreme temperatures necesssarily involves an animal in some other disadvantage, such as extra consumption of energy,

or other metabolic stress. If this were so, then an ability to acclimatize would be of real value in the terrestrial environment, where short and long term temperature changes occur over a wider compass than they do in water.

(iii) Rates of transpiration

As regards comparative rates of water loss in *Uca*, the results shown in figure 3, tentative as they are, suggest that the order in which the species stand in this respect corresponds with their order in respect of terrestrialness of habitat, with the exception of *inversa*, which at first loses water rapidly—though after half an hour or so the rate of loss is least of all.

The ability to restrict loss of water is certainly of value to a terrestrial animal. It is well known that many insects have developed such an ability very fully. Woodlice, although they vary in this respect, lose water more rapidly than most insects (Edney, 1951, 1954). Rates of loss from woodlice vary from 2·7% (*Armadillidium vulgare*) to 10·6% (*Ligia oceanica*) of original weight per hour at 32 °C. in dry moving air. Comparable figures derived from the present work are 1·7% (*Uca annulipes*) and 5% (*Uca marionis*) in still dry air at 25 °C. Even if we double these rates to allow for the slightly lower temperatures and the still air, the figures for fiddler crabs are no higher than those for woodlice. It seems, then, that the risk of desiccation on land is no more severe for fiddler crabs than it is for woodlice, assuming that the lethal levels of water depletion are approximately equal. Such lethal levels have not yet been determined for *Uca* spp. and indeed the determination is not simple because drying out of the gills and carapace may cause death by asphyxiation (as it does in woodlice (Edney & Spencer, 1955)). The only comparable figures in respect of other crabs are those of Bliss (personal communication), who found that the losses of weight (presumably water) at death in *Gecarcinus lateralis*, *Cardisoma guanhumi* and *Ocypode albicans* were 21·6%, 16·3% and 12·5% respectively. *Gecarcinus* lived for 91 days in air at about 78% R.H., *Cardisoma* for 59 days, and *Ocypode* for 20 days in these experiments, so that it is not clear whether *Gecarcinus* (which is the most terrestrial of the three) suffered greater loss of weight before it died because it could tolerate such a loss or whether the other species died sooner because of respiratory difficulties. It would be interesting to sort out these possibilities in the above species and also in *Uca*.

(iv) Transpiration and body temperature

A significant reduction in body temperature as a result of transpiration has been shown to occur in *Uca* spp., both in the laboratory and in nature, and there can be little doubt that this process is of value to the crabs concerned, for the field data strongly suggest that they are often exposed to environmental temperatures which would otherwise prove fatal. There are, of course, retreats into which the crabs can retire, where temperatures are less extreme; yet they do spend a lot of time upon the surface, feeding and at times arranging for sexual action (Altevogt, 1957, 1959; Crane, 1947, 1958), so that the ability to stay out longer probably confers survival

value. Dembowski (1926) claims that *Uca* can remain alive in air for two weeks without changing the water in the gill chambers.

However, we must remember that a depression of body temperature means a loss of water, and that the ability to lose water rapidly, although it confers an immunity to high temperatures for short periods, is not a character of any permanent value to a really terrestrial animal. On balance an ability to conserve water is much more important. It has been suggested elsewhere (Edney, 1954) in connexion with the evolution of terrestrial isopods, that the littoral environment as a step towards land life may have this disadvantage, that it confers a high survival value on the ability to transpire rapidly, both for temperature control and for respiration, and that because of this the crustacean inhabitants of the zone may have reached an evolutionary cul-de-sac. The present results do nothing to contradict this view.

There is, perhaps, one way out of this difficulty: an animal which possessed the ability to transpire rapidly for a short period of time, and then to conserve water strongly, would be at a great advantage. The present results are too few to support such a claim, but what figures we have for *Uca inversa* suggest that this crab may behave in such a way. The results for rates of loss (fig. 3) and for body temperature (figs. 4 and 6) are consistent with this view.

(v) Osmotic relationships

The osmotic properties of littoral crustaceans in relation to terrestrial life have been considered by Edney (1960) and by Robertson (1960). Jones (1941) showed that the blood of *Uca crenulata* is isotonic with 85% sea water, and that the crab regulates osmotically in both dilute and concentrated sea water. Gross (1957a) found that oxygen consumption in this crab was somewhat higher in greater osmotic stresses, but he found no evidence to suggest that such increases in metabolic rate were caused by additional osmotic work. Teal (1958) found that *U. minax* preferred fresh to salt water while *U. pugnax* and *pugilator* preferred salt, and he was able to point to this difference as one of the factors determining the local distribution of the three species.

The results of the present immersion trials suggest that it is more difficult for *Uca annulipes* to resist osmotic stress in concentrated sea water than in 50% sea water (although this is farther from its blood O.P.) or indeed than in fresh water.

The water in which *Uca* spp. are immersed at Inhaca is somewhat hypotonic to sea water, but very variable (MacNae & Kalk, 1958). The habitat is flooded at least by high spring tides, but fresh water seeps in from the surrounding country. Osmotic problems posed by this environment deserve further study, but we now know at least that *Uca annulipes* can live for a minimum of 11 days in 50% sea water and below even though entirely submerged.

The present results need not be discussed further, but a brief consideration of the significance, if any, of osmoregulatory powers in so far as littoral animals are concerned, may be useful.

Strictly speaking, there is no osmotic problem for land animals, since there is no external aqueous medium—the problem is one of water retention. The question

to be answered, then, concerns the extent to which osmotic requirements of the littoral zone call forth osmotic mechanisms which are of value also in a terrestrial environment. Most littoral crabs are good osmoregulators (Jones, 1941). Hypo-regulation involves the secretion of salt against a gradient and is therefore adaptive for land life. For a land crab, hypo-regulation might also prevent water loss to concentrated fluids in the gill chamber, the concentration itself having been caused by evaporation of water from that area. But Gross (1955) points out that the volume of water in the gill chamber is so small that even if all its salts were absorbed, this would cause but little change in the blood O.P.

The ability to hyper-regulate, valuable indeed in estuarine crabs, may also be of importance to a land crab when it burrows into sand and meets fresh water, but not otherwise. Many littoral crabs are to some degree euryhaline, and this may be of value to a land animal, either if it cannot regulate its internal O.P., or by reducing the osmotic gradient against which regulation must take place.

(vi) General

As a result of his work on *U. minax*, *pugnax* and *pugilator* in salt marshes, Teal (1958, 1959) was able to point to certain environmental factors as probably being involved in determining the local distribution of the crabs. These were: salinity preferences, substrate preferences and the ability of *pugnax* and *pugilator* (but not *minax*) to acclimatize in respect of the effect of temperature on metabolic rate. Interspecific repulsion, which he also demonstrated, probably serves to accentuate the territorial boundaries.

Teal believes that the ability of *pugnax* and *pugilator* to acclimatize is responsible for the occurrence of these two species alone in the warmer salt marshes. He found no evidence that upper lethal temperatures differed and concluded that they could not be involved in determining local distribution.

It is likewise one of the purposes of the present work to account for local distribution of *Uca* spp. in mangrove areas. This aim has as yet by no means been achieved. What has been found is that in laboratory conditions, the several species of fiddler crabs studied do possess physiological properties which might very well be adaptive to varying degrees for land life. But apart from the few measurements of temperature made in their natural habitat, we know very little about the significance in the field of these properties. So far as they go, the present results suggest that the upper temperature limits of the various species may be important in determining distribution at Inhaca. Unlike Teal's species, these crabs show significantly different upper lethal temperatures and they seem to approach these limits in the field. But the temperatures encountered at Inhaca were higher than those reported by Teal, whose highest measurement was 45 °C. on the marsh surface, and then no crabs were about. It is possible that different sets of factors will prove to be involved in determining local distribution in different parts of the world-wide range of *Uca* spp.

Perhaps the most urgent need now is for more information about the environment and the responses of the crabs in it. For example, information is needed about the

length of time that crabs spend in the open and about the amount of water they lose in so doing. We also need to know something about the site of water loss (whether from the gills or elsewhere) and the effect of this upon the body fluids. How much water may be lost without permanent injury and what is the nature of such permanent injury? To what extent, if at all, does cutaneous respiration occur, and is it affected by water loss? What is the oxygen content, reaction and osmotic pressure of the water in the crabs' holes, and are they perhaps forced out to breath? These are some of the questions that need answering before we can say anything useful about the factors which limit the distribution of the various species to their various habitats in tropical mangrove swamps. It is only when these factors are fairly well understood that we shall be able to pronounce upon the possibilities from an evolutionary point of view offered by the mangrove swamp environment as a means of attaining fully terrestrial life.

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ANIONIC OXYGEN THE BUFFER BASE OF THE MITOCHONDRIA

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It is suggested that anionic oxygen, formed by the transfer of electrons from cytochrome oxidase to molecular oxygen, functions as a strong base, i.e. as a H^+ ion or proton acceptor of great physiological significance.

In accounts of physiological acid-base balance the following buffer bases of the body fluids are usually considered: HCO_3^-, HPO_4^{2-}, and protein anions including haemoglobin, Hb^- and HbO_2^-. But, the existence and specific function of anionic oxygen, perhaps the most important intracellular buffer base, have been overlooked.

Anionic oxygen is formed at the end of the respiratory chain of electron transfer systems when electrons from the ferrous atom of cytochrome oxidase are transferred to molecular oxygen. Molecular oxygen is thus reduced to anionic oxygen. According to the hypothesis of G. N. Lewis molecular oxygen is an acid because it is an electron-pair acceptor. By accepting electrons from Fe^{2+}, molecular oxygen is thus not only reduced but, and this is the important point which is usually overlooked, it is converted into a base, i.e., according to the Bronsted concept, into a substance which is a H^+ ion or proton acceptor.

In the course of metabolism large quantities of hydrogen atoms are produced, especially in the citric acid cycle. In the mitochondria hydrogen atoms $(2H^+ + 2e)$ are transferred from the substrate to a pyridine-nucleotide coenzyme and then to a metalloflavoprotein coenzyme. The reduced form of the latter transfers electrons to the cytochromes and sends hydrogen ions into the solution. This would cause a disastrous increase in hydrogen ion concentration within the mitochondria were not the hydrogen ion immediately neutralized by the strong base, anionic oxygen, formed by the transfer of electrons from the Fe^{2+} of cytochrome oxidase to molecular oxygen. It is well known that molecular oxygen has the highest oxidation-reduction potential and therefore the highest electron affinity of all systems in the cell.

The two associated hydrogen atoms transferred from the substrate can be regarded as a weak Lewis base. Molecular oxygen is a weak Lewis acid. The transfer of electrons to molecular oxygen converts the weak base to a strong acid (H^+) and the weak acid to a strong base.

The reactions of the electron transfer system take place in the mitochondria. Because of its site of action, its availability in large quantities and its property as a strong base, anionic oxygen must be regarded as the most important buffer base of the cell.

Its quantitative importance is apparent from the following calculation: The oxygen consumption at rest is 250 ml/min. which is equivalent to 0.011 moles O_2/min.

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which in turn is equivalent to 0.022 moles anionic oxygen/min. This combines with 0.044 moles H^+/min., i.e. 63.4 moles H^+/day. This is equivalent to 6.34 litres of concentrated hydrocholoric acid.

The total production of all other acid end products of metabolism, mainly carbonic acid, is equivalent to 3 litres of concentrated hydrocholoric acid per day.

The bicarbonate, phosphate and protein systems buffer the acids liberated into the body fluids. On the other hand, anionic oxygen has the specific function of neutralizing the hydrogen ions produced in the mitochondria.

It may be pointed out that carbon dioxide, produced in large amounts by cells, gives rise to the chief buffer base of the extracellular fluid, i.e. HCO_3^-. Similarly oxygen, taken up in large amounts by cells, gives rise to the chief intracellular buffer base, i.e. anionic oxygen.

The above hypothesis suggests an explanation for the fact that a lack of oxygen or the injection of a trace of cyanide leads to hyperventilation. In each case the lack of anionic oxygen would lead to an intracellular accumulation of hydrogen ions.

Oxygen brought to the cells via the lungs and the bloodstream thus performs two major functions. First, by accepting electrons, it oxidizes ferrous cytochrome to ferric cytochrome so that the latter can again accept the electrons which are continuously being produced by the oxidation of the substrates. Secondly, by accepting electrons it is converted into a buffer base of great physiological significance.

THE LENGTH AND INCLINATION OF THE PRIMATE CERVICAL SPINOUS PROCESSES

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The relationship between the length of the cervical spinous processes and the inclination of the spines, the size of the vertebrae, the depth of the excavations on the superior aspect of the vertebral bodies, the inclination of the articular facets, the length of the nuchal plane and the size of the skull and the position of the head were studied in 270 specimens of different primate species. In addition the individual sexual ranges of variation of these measurements were determined. Certain conclusions on the factors affecting head balance and the specialization of man were drawn.

Through the generous help of the South African Council for Scientific and Industrial Research I was able to study a large series of primate cervical vertebrae in the Anthropological Institute at the University of Zürich during 1956. The material, with few exceptions, is the property of the Director of the Institute, Professor A. H. Schultz. The remaining material belongs to the anthropological collection of the University.

I am much indebted to Professor Schultz for allowing me to work in his institute and wish to thank him most cordially for his help and the facilities he put at my disposal. Twenty-three baboon skeletons were also measured at the Anatomy Department, University of the Witwatersrand, with the very kind permission of Professor R. A. Dart.

The present paper deals chiefly with the spinous processes. I was particularly interested in the relationship of the length of the spines to the way the head is carried on the spinal column. The varying postures adopted by the various primate species represent most instructive experiments for the study of this problem. In addition the relationship between the length and inclination of the spines to the size of the vertebral body, the angle of the articular facets, the length of the nuchal plane of the skull, etc. were considered.

The species investigated and the number of individuals measured are listed in table 1. A total of 270 specimens were examined.

1. Among the extant primates the spinous processes attain their maximum development in the Pongidae and in the potto (Prosimian), whereas they are least developed in the Tupaidae and the Lemuridae.

The length of the spines in the Pongidae is subject to extensive sexual dimorphism. On an average the lengths of spines in female gorillas are only 66% of those

TABLE 1

Species	Numbers and sex of adult specimens measured		Species	Numbers and sex of adult specimens measured	
	Male	Female		Male	Female
Homo sapiens	36		Alouatta palliata	2	–
Pan troglodytes	5	9	Saimiri oerstedii	4	1
Gorilla gorilla	7	4	Cebus capucinus	5	–
Pongo pygmaeus	3	4	Ateles geoffroy	2	1
Hylobates lar	24	21	Lagothrix lagotricha	1	–
Symphalangus syn.	7		Leontocebus geoffroyi		56
Macaca sinica	2	–	Tupaia chinensis	2	3
Macaca mulatta	8	12	Lemur macaco	1	–
Papio sphinx	2	–	Hapalemur	1	–
Cercocebus torquatus	–	2	Lepilemur	1	1
Cercopithecus aethiops	5	3	Microcebus	2	1
Cercopithecus cephus	1	–	Propithecus	1	1
Cercopithecus nictitans	1	–	Daubentonia	–	1
Erythrocebus patas	1	–	Nycticebus	2	4
Presbytis cristatus	2	1	Loris	–	1
Presbytis rubicunda	1	–	Perodicticus potto	–	2
Presbytis entellus	1	1	Galago senegalensis	1	–
Nasalis larvatus	1	1	Galago crassicaudatus	1	
Aotus trivirgatus	1	2	Tarsius bancanus	1	–
Alouatta seniculus	1	–	Tarsius syrichta	–	2

The nomenclature used here is that proposed by Fiedler 1956.

of the male; in the orang-utan the corresponding figure is 72% and in the chimpanzee it is 88%. In *Hylobates* there is no difference due to sex as is also the case in those other primates where this could be determined.

The length of the spine also varies considerably among specimens of the same species. In 3 adult male *Pongo* specimens the shortest spine of a C_5 is 30% less than the longest spine. The ranges of variations in the lengths of the spines in man and the chimpanzee overlap, but both are outside the range of variation of the gorilla and the orang-utan. The spinal lengths also overlap in the two latter forms.

2. The position of the longest cervical spines in the gorilla and orang-utan differs greatly from that of all the other primates measured. In these two forms the length of the spines increases rapidly from C_2 to C_4, C_5 or C_6, with a more gradual decrease to C_7 and T_1. In the other primates the 3rd, or sometimes the 4th, cervical spine is usually the shortest with a gradual increase to C_7 or T_1.

The chimpanzee occupies an intermediate position in this respect since the last cervical spines are all practically of the same length. In a few other specimens, *Nasalis larvatus*, *Aotus*, *Alouatta seniculus* and *A. palliata*, the spine of C_2 is shorter than that of C_3.

No sexual dimorphism was noticed in the position of the longest spines but individual differences are marked, as can be observed from table 2.

3. The *relative* length of the spine has greater differential importance as it permits direct comparison between species of different size. The size of the vertebral body (represented by its minimum transverse diameter + its antero-posterior

The Length of the Cervical Spinous Processes

Table 2

	Homo Male			Pan Male			Pan Female			Pongo Male			Pongo Female			Gorilla Male			Gorilla Female		
	min	max	avg	min	max	avg	min	max	avg	min	max	avg	min	max	avg	min	max	avg	min	max	avg
C2	12	27	18	16	24	18	14	20	17·4	24	33	28	20	33	27·3	25	43	33·1	21	33	26
C3	11	29	15·7	16	35	23·6	17	28	21·2	36	50	43	18	38	29	43	90	76	41	58	48
C4	10	23	16·1	24	29	27·4	21	31	24·4	40	60	50	26	41	33	61	97	86·9	46	62	55·3
C5	13	29	20	28	30	31	23	33	26·6	44	63	53	31	40	35·3	85	98	91·6	49	64	57·3
C6	13	32	24·7	32	41	36·4	25	34	30·1	48	62	53·3	33	39	36	84	95	89·2	50	64	56·8
C7	23	38	32·9	34	44	37	26	36	31·7	46	59	51	31	36	33·7	68	88	79·8	47	57	51·3
T1	28	47	36·2	34	42	36·8	27	37	32·1	40	49	44	26	33	30	54	77	69·5	43	51	45·7

	Aotus Male			Aotus Female			Alouatta Seniculus Male	A. Palliata Male			Nas. Larvatus Male	Nas. Larvatus Female
	min	max	avg	min	max	avg		min	max	avg		
C2	3·5	3·5	3·5	3	3·5	3·3	16	10	10	10	12	9
C3	3	3	3	4	4·5	4·3	17	11	13	12	13	5
C4	—	—	—	3	3	3	18	11·5	12	11·8	—	8
C5	4	4·5	4·3	2	2·5	2·3	19	11·5	14	12·8	—	8
C6	5	7·5	6·3	5	5·5	5·3	21	16	16	16	—	9
C7	6	8	7	6·5	7·5	7	23	19	20	19·5	20	13
T1	—	—	—	7	8·5	7·8	25	20	20	20	20	15

Minimum, maximum and average length of cervical spines. For number of specimens measured, see table 1.

diameter) as a representative of the size of the body of the animal (Schultz 1953) was selected as a basis for comparison.

The cervical vertebral bodies increase in size from C_3 or C_4 to T_1 in the simians measured. This increase is mostly due to an increase in the transverse diameter. In the Pongidae the a–p diameters (= dorso-ventral diameter in quadrupedal position) are very similar from C_2 to C_7, except in the gorilla and to a lesser extent the chimpanzee where it is slightly less in the first and last numbers of the series.[*] The body of C_2 is always bigger than that of C_3 and (mostly) C_4. In the Cercopithecoidea the a–p diameter is also very similar from C_2 to C_7, being only slightly less in the middle cervical vertebrae than in C_2 (where the transverse diameter is less than that of C_3), C_6, C_7 and T_1. However, in the Ceboidea there is a tendency for the a–p diameter to decrease from C_2 to T_1. The decrease is not enough to offset the increase of the transverse diameter and there is therefore a progressive increase in size of the vertebral body from C_3 to T_1 in these forms.

In the few prosimians in which these measurements could be taken, the increase in transverse diameter is cancelled by the decrease in a–p diameter. There is therefore hardly any increase in body size except at T_1. In the potto the middle bodies are slightly smaller.

The general increase in spinal length from C_3 to T_1 (*vide supra*) can therefore be correlated with the corresponding increase in the size of the vertebral body. The body of C_2 is bigger than that of C_3 and/or C_4 and carries a spine that, even in those specimens in which it is not longer than those of C_3 and C_4, are always thick and sturdy. The middle spines in the potto are also shorter (except C_2), in harmony with the smaller bodies.

On the other hand in the other prosimians in which well-developed spines are present (e.g. *Niciticebus*; *Propithecus*) there is no increase in body size to accompany the increase in spinal length. In the gorilla and pongo the tallest spines are carried by C_5 and C_6 which have bodies that are smaller than those of C_7 and T_1. The latter bodies carry relatively short spines.

Spines that are very long in relation to body size $\left(\dfrac{\text{length of longest spine} \times 100}{\text{size of vertebral body}}\right)$ are found particularly in the gorilla, (C_5, 237% male, C_4, 180% female), *Pongo* male (C_4, 144%), Chimpanzee male (C_6, 125%) compared to *Symphalangus* (C_4, 74%) and *Hylobates lar* (T_1, 76·5% female; C_7, 73% male). Marked sexual dimorphism is only apparent in the gorilla and the orang-utan, the females having relatively shorter spines. (Table 3, last column.)

Relatively long spines in the Cercopithedoidea are found in the males of *Papio sphinx* (T_1, 113%) *Cercopithecus* (*C. aethiops* male, T_1, 119%; female T_1, 109%; *C. nictitans* male T_1, 113%). The shortest spines are found in *Presbytes rubicundus* (male T_1, 69%).

Among the New World Monkeys the relatively longest spines are found in the

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[*] According to Francis (1955) the a–p diameter in the Negro and White skeletons based on large series are very similar from C_2 to C_7. In both groups the measurement for C_7 is slightly less than that for C_4.

TABLE 3

		Spinal/Nuchal index	Condylion index	Prosthion index	Max. spinal index
Gorilla	Male	107	93·9	+11·2	237%
	Female	109·2	93·3	−1·6	180%
Chimpanzee	Male	82·5	88·4	+6·7	125%
	Female	77·8	88·3	+5·9	105%
Pongo	Male	114	95·3	+28	144%
	Female	78	91·8	+17	C₄ 120%
Hylobates	Male	60·6	91·0	+7	73%
	Female	60·9	87·2	+6·4	76·5%
Symphalangus		85	90·8–93·8	+12·2–14·2	74%
Papio sphinx	Male	74·5	95·4	+26·3	113%
	Female	—	86·7	−5·2	—
Cercopithecus aethiops	Male	45·7			119%
	Female	44			109%
C. nictitans	Male	—			113%
	Female	45			
Alouatta seniculus	Male	119			124%
	Female	—			
A. palliata	Male	134	95	+32·7	115%
	Female	—	93	+24	—
Ateles	Male	71·5	84·4	+5·6	153%
	Female	61	84	+6·3	127·5%
Saimiri	Male	38	78·4	−6·3	114%

Comparison between spinal/nuchal, condylion, prosthion and spinal indices of some primate species. The middle two indices are after Schultz 1955.

Alouatta species (Male *A. seniculus* T_1, 124%; male *A. palliata* T_1, 115%) and *Ateles* (male C_6 153%; female C_6 127·5%).

4. The concavity of the superior surface of the bodies of the cervical vertebrae is relatively much less in Man than in the other primates measured. It attains its maximum development (relative to the size of the vertebral body) in the chimpanzee. In the Pongidae the concavity is very deep and absolute differences in depth can be more accurately measured. A marked sexual difference is observed in these forms. The superior surfaces of the bodies are more deeply excavated in the males than in the females. The individual variation is considerable and overlapping of the ranges occurs between, for example, Man, chimpanzee and gorilla (table 4).

The length of the spine is not correlated with the depth of the excavation on the superior surface of the vertebral body. The depth of these surfaces in, for example, C_4, C_5 and C_6 which carries the tallest spines in the gorilla, is not greater (or less) than in C_3 and C_7 which have relatively shorter spines. The very deeply excavated superior surfaces are restricted to the cervical region. In T_1 the depression is much shallower and may even be absent as in some gorilla specimens.

5. The length of the nuchal plane (measured from opisthion to inion) was compared with the length of the tallest spines. In the gorilla (male and female) a good correlation was observed. The longest spines are (on the average) 109·2% (female) and 107% (male) of the nuchal length. In the chimpanzee (82·5%, male; 77·8%, female), *Pongo* female (78%) and Symphalangus (85%) the spines are

TABLE 4

Vertebral No.	PAN						GORILLA						HOMO		
	Male			Female			Male			Female					
C_3	6	8	7	5	7	6	5	8	7·2	4·5	7	5·5	3	7	5·2
C_4	6	8	6·7	5	7	6·2	7	9	7·7	4	7	5	3	7	5·3
C_5	7	9	8	4·5	7	6·3	6	8	6·5	2	4	3	4	7	5·5
C_6	6	8	7	5	7	6	5·5	8	6·4	2	6	4·3	4	8	6·1
C_7	7	7	7	5	7	6	3	8	6·2	4	5	4·5	4	7	5·3
T_1	—	—	3	2	4	2·2	0	5	2·6	—	—	2	2	7	4·2

Minimum, maximum and average depths of the notches on the superior surfaces of the vertebral bodies.

relatively much shorter and in *Hylobates* (*H. lar* male, 60·6%; female 60·9%) it is very much less. However, in the *Pongo* male the spinal length is considerably more than the length of the nuchal plane, (114%). In the remaining simiae T_1 usually carries a taller spine than C_7 and the length of the former was therefore used, when necessary, in the comparisons. Fairly good correlations were obtained in the larger species but in the smaller species the spines were relatively much shorter (table 3).

In, for example, *Presbytis*, a genus which includes both large and small spined types, the larger species (*P. entellus*) has an index of 82 compared with 47 (female) and 48·5 (male) in *P. cristatus* and 42 (male) in *P. rubicundus*.

In the prosimian species in which the spines are well developed, there is a very close correlation between the two measurements. The exception is the potto in which

TABLE 5

Relationship between spinal length, nuchal length and skull size in the baboon *Papio comatus*.

Spinal length (T_1)	Nuchal length	Skull size	
		Total length	Total width
14	32	174	97
20	31·5	159	93
20·5	38	180	102
21	31	172	98
21	32	185	101
22	30	157	93
22	28	164	93
22	30	171	99
22·5	36	172	97
23	32	172	98
23	30	177	102
23	36	177	103
23·5	31	174	100
23·5	33	170	94
24·5	34	179	101
25	37	188	94
27	35	188	97
27	38	209	111
27	40	222	125
28·5	43	218	117
32	38	209	111
36	38	219	125

the spines are remarkably developed; they project above the level of the skin (Hill 1953) and are apparently used for protective purposes.

To assess the range of individual variation in spinal length and the effect of the size of the skull in a single species, the spinal and nuchal lengths of 23 baboons of both sexes were measured in the Department of Anatomy, University of the Wit-watersrand. In addition the lengths and widths of the skulls were also measured (table 5).

From these measurements it is clear that there is a general—though not absolute—correlation between spinal and nuchal length. These two measurements are correlated with the size of the skull. However, two specimens, each with a nuchal length of 38 mm., have spinal lengths of 27 and 36 mm. respectively.

The Inclination of the Spines

The angle of the spine is measured between a line passing through the root of the spine (where it meets the neural arch anteriorly) and the middle of the tip of the spine and a line passing along the anterior (or ventral) surface of the body of the vertebra. In short (and particularly in deep) spines the measured angle is usually more than its true inclination. Although the short anterior spines are therefore tabled (table 6) as having fairly acute angles this might not be a true reflection of their direction as indicated by the superior (or anterior) border of the spine. However, the latter border is not always a straight line (Toerien 1957) and therefore cannot be used for determining the angle.

The spines of the middle cervical vertebrae are usually more perpendicular to the anterior surface of the vertebral body than are the spines of the posterior cervical vertebrae. *Symphalangus* and *Hylobates* differ from the other measured species in having the spine of C_7, less inclined than those of the middle cervical vertebrae. In Man C_6 is the least inclined. In the gorilla the anterior spines are directed slightly cranially. Middle cervical spines that are cranially directed are not uncommon, e.g. in *Macaca* and *Papio sphinx*. The most inclined spines occur in Man and (even more markedly) in the New World Monkey, *Alouatta*.

In the forms in which enough individuals of both sexes could be measured the spines of the males appear to be less inclined than those of the females although the middle spines of at least one species (*Hylobates lar*) are more acute in the male.

Individual differences are considerable (table 6). This is particularly well illustrated in Man who (with the exception of *Alouatta*) has the most inclined spines but their angles overlap with those of the chimpanzee which have very nearly perpendicular spines.

As a rule the longest spines (last number of the series) are also the most inclined. Exceptions are found among the Pongidae in which the middle spines are the longest and least inclined and in *Symphalangus* and *Hylobates* in which the last cervical spines are the longest and the least inclined.

The inclination of the superior articular facets is measured by the angle between

TABLE 6

	HOMO			PONGO Male			PONGO Female			GORILLA Male			GORILLA Female			PAN Male			PAN Female		
♂	−17	55	27·7	2	8	5	0	18	5	−20	4	−7·7	−15	5	−7	7	12	9·5	−2	25	14·9
♂	−14	45	31·5	2	9	5·5	3	10	5·7	−11	2	−5·	−5	6	−2	3	9	6	12	24	17·4
♂	−8	48	33·1	0	−8	4	−3	10	5·7	−11	5	−1·6	−4	8	·05	6	6	2	3	18	11·8
♂	−12	45	28·6	−4	6	1	−1	11	8·5	−9	5	·2	−3	8	3·8	−3	9	3	8	13	10·7
♂	−10	40	22·4	10	18	14	7	16	11	−9	13	3·2	−8	8	4	0	15	7·5	6	17	1·7
♂	−19	36	27·8	15	19	17	15	22	16	−2	17	4·8	−2	12	6·3	15	25	17	16	18	16·8
T₁	−19	37	29·8							−3	24	6·7	13	22	19	20	17·5		21	30	23·8

	HYLOBATES LAR Male			HYLOBATES LAR Female			MACACA MULATTA Male			MACACA MULATTA Female			PAPIO SPHINX			ALOUATTA PALL.			SYMPHALANGUS		
♂	−7	6	1	6	9		22	40	7·5	13	43	29·1	−4	23	9·5	24	38	31	0	35	18·9
♂	−7	25	18	17	22		10	33	19·5	−3	27	21·3	0	22	11	32	34	33	18	25	24·1
♂	−9	20	15·3				1	12	14	−5	22	5·9	−6	7		22	24	23	9	30	18·9
♂	−	−	24				−3	15	24	−5	25	7·8	−3	2	·5	19	20	19·5	12	25	18·6
♂	−9	24	16				−2	11	11	2	28	5·8	0	−6		12	29	20·5	5	17	12·3
♂	−5	15	9·7				3	22	18	5	33	9	−2	10	3	19	26	22·5	3	20	9·8
T₁	20	31	25·5				4	22	42	5	38	13·4	17	17	4	37	39	38	17	27	22·7

Minimum, maximum and average spinal angle of some primate species.

a line passing along the surface of the facet and a line passing along the anterior (or ventral) aspect of the body of the vertebrae.

The angles of the facets of corresponding cervical vertebrae are very similar in the various forms measured. The facet of C_2 is usually horizontal ($0°$) or slightly reversed compared with those of the succeeding vertebrae. C_3 is placed fairly obliquely; the middle vertebrae less obliquely, whereas the facet of C_7 is usually and that of T_1 always more inclined than in C_3.

This sequence is subject to some variation. The relatively lower angle of the facets of the middle vertebrae are particularly well observed in the Hominoidea and the Old World Monkeys. In *Presbytes rubicundus*, *P. cristatus* and *Cerocebus torquatus* the angles of the facets of the middle vertebrae are only very slightly less than those of C_3, whereas they are more inclined than in C_3 of *Nasalis larvatus*. This is also true of the majority of the New World Monkeys although in *Saimiri* and *Leontocebus* the facets of the middle vertebrae are less oblique than in C_3. The facets of the middle vertebrae are most inclined (in all the primates measured) in the two *Alouatta* species (*A. palliata* and *A. seniculus*).

A rough correlation exists between the angle of the spine and the angle of the articular facets. As a rule the middle cervical spines (*vide supra*) and the middle facets are less inclined than those of the last cervical vertebrae. In *Ateles* when the inclination of the spines tends to increase gradually from C_2 to T_1 (except C_6 in the male) the facets show a similar gradual increase in inclination. On the other hand in *Symphalangus* and *Hylobates* the spine of C_7 is the least inclined whereas the angle of the facet of C_7 is much more acute than in the middle vertebrae.

<div align="center">DISCUSSION</div>

Head balance and length of cervical spines

In specimens of the Hominoidea with relatively heavy heads, protruding faces and occipital condyles that are placed far backwards, the cervical spines are very well developed. In the orang-utan male where the condyles are situated farthest aborally among the Pongidae, the face is very protruding and the head is relatively very heavy ($12·3\%$ of total weight (Schultz 1955)). These cranial features are correlated with the very long cervical spines of orang-utans in relation to both the nuchal length of the skull and the sizes of the cervical vertebral bodies in that ape. Gorillas have a similar combination of features. *Symphalangus* also resembles these two apes in these respects but the spines are not very long in relation to the size of the vertebral bodies.

On the other hand in *Hylobates* the condyles are placed far forward, the face is short and the head is only $7·2–7·5\%$ of the body weight (Schultz 1955), and the spines are relatively very poorly developed. This combination of features is also found in the chimpanzee although it is not so marked. In the *Hylobates–Pan* group also the angle of the spines is more acute than in the male *Pongo–Gorilla* group. According to Slijper the ligaments suspending the heads in mammals run more or less perpendicular to the long axes of the spines. The heads of the second or *Hylobates–*

Pan group therefore must be carried at a higher level than at least the middle cervical vertebrae in the quadrupedal position. The anterior part of their cervical vertebral columns must therefore be curved dorsally, supporting heads that are perched on top of more vertical spinal columns and not hanging from horizontal columns.

Among the Hominoidea, Man is outstanding in the shortness and obliquity of his cervical spines and his low condylion and prosthion indices (Schultz 1955).

The remaining primates are not naturally divided into two such groups. For example in both *Papio sphinx* and *Alouatta*, which have very high condylion and prosthion indices (Schultz 1955), the spines are relatively long compared with the size of the cervical vertebral bodies. However, only in *Alouatta* are the spines long relative to the length of the nuchal plane. In the latter genus the spines are very oblique whereas they are perpendicular in *Papio*. In *Ateles* the spines are relatively (to vertebral body size) very long but they are very oblique and the prosthion condylion and spinal-nuchal indices are lower than in *Papio* and *Alouatta*. In *Saimiri* in which the prosthion and condylion indices are very low, the spinal-nuchal length is the lowest among the primates (38%), the spines are relatively oblique and long relative to the vertebral body size.

The distinctiveness of Man

The cervical column of Man differs from that of the anthropoids in (1) the relative shortness of the spines, (2) the deeply notched superior surfaces of the bodies (Martin 1928), and (3) the obliqueness of the spines (Boule and Vallois 1957).

The range of variation in the angles of the spines of Man and the chimpanzee and their overlap was dealt with elsewhere (Toerien 1957). The lengths of the spines and the depth of the notches on the superior surfaces of the bodies overlap considerably in these two forms. The same applies to the sequence of increase in spinal length from C_2 to C_7. In the length of the spines (of C_7) relative to the length of the nuchal plane Man also does not differ from, for example, the chimpanzee and the gibbon.

The relative shortness of the spines in Man and some other primates (*Cercopithecus*, *Saimiri*, etc.) is not only related to the position of the skull on the vertebral column but allows much greater freedom of movement in the cervical region. It is obvious that posterior curvature (or extension) of the neck is mechanically impossible between the middle cervical vertebrae of the gorilla. In the chimpanzee, gibbon, siamang and particularly in Man the anterior cervical spines are considerably shorter to allow greater posterior curvature (or increased extension) of the neck. In Man the cervical column develops an intrinsic curvature and extension movement is further facilitated by the relatively shallower superior surfaces of the cervical vertebral bodies.

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GEOMAGNETIC OBSERVATIONS ON MARION ISLAND, GOUGH ISLAND AND TRISTAN DA CUNHA*

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In September 1957 the International Association of Geomagnetism and Aeronomy recommended that a magnetic secular variation station be established on Tristan da Cunha (37°03′ S., 12°18′ W.). During the ensuing three years the Union of South Africa has established secular variation stations on no fewer than three of the southern islands, viz. Tristan da Cunha, Gough Island (40°20′ S., 9°55′ W.), and Marion Island (46°51′ S., 37°52′ E.). As all three islands are composed of highly magnetic material, it is essential that the points at which the initial observations were made be exactly reoccupied during future surveys. The stations (two on each island) were accordingly clearly marked, and a careful record was kept of the height above ground-level at which each observation was made. The results of the magnetic observations carried out on the three islands in 1960 are presented in full. It is recommended that the stations be reoccupied at intervals of about five years.

I. Introduction

The secular variation of the Earth's magnetic field has important applications in magnetic cartography and in problems concerning the deep interior of the Earth. Our knowledge of the secular changes is based partly on the continuous records of magnetic observatories and partly on periodic observations at carefully marked field stations. While the distribution and average density of magnetic observatories and repeat stations over the larger land areas may be regarded as reasonably satisfactory, the paucity of magnetic stations in the ocean areas and polar regions renders the over-all picture far from complete. Recent advances in observational technique, such as the use of airborne magnetometers for large-scale magnetic surveys, tend to enhance rather than to detract from the importance of permanent ground-stations.

The need for a detailed study of the secular changes, on a regional as well as on a planetary basis, is as great as ever. Among the resolutions adopted by the XIth General Assembly of the International Union of Geodesy and Geophysics in September 1957 (IUGG, 1957), we note the following:

'The International Association of Geomagnetism and Aeronomy, considering the importance of a better knowledge of the magnetic secular variation in the region of pronounced foci in the South Atlantic between the coasts of South Africa and South America, and in view of the favourable position of Tristan da Cunha for an investigation of this phenomenon, recommends the

establishment at an early date of a good magnetic repeat station on that island.'

The proposal which led to this resolution had been drafted jointly by Professor Slaucitajs of the Universidad Nacional de la Plata, and Col. J. J. Boonzaaier, Director-General of Surveys, Union of South Africa. As the idea had originated in the Argentine, it seems fitting that South Africa should have taken the initiative in putting the recommendation into effect.

The action taken by the Union Government will enable its delegates to report to the IUGG Assembly in July–August 1960 that secular variation stations have been established on no fewer than three of the southern islands, viz. Tristan da Cunha, Gough Island and Marion Island (fig. 1).

The projects were carried out during relief voyages to the meteorological stations maintained on these islands by the Department of Transport, Union of South Africa.

As all three islands are composed of highly magnetic material, it is essential that the points at which the initial observations were made be exactly reoccupied during future surveys. The stations (two on each island) were accordingly clearly marked, and a careful record was kept of the height above ground-level, h, at which each observation was made.

Due to the very limited time available at Gough and Marion, the azimuths of the reference marks used for the declination measurements could not be determined with the required accuracy. In the results given at the end of this paper, the declination (D) is accordingly expressed in the form

$$D = C - M$$

where M is the magnetic azimuth and C the true bearing.

II. Tristan and Gough, 1958

The establishment of the magnetic secular variation stations on these islands in 1958 was undertaken jointly by the Hydrographic Office of the South African Navy and the Magnetic Observatory, Hermanus (Gilman and Scheepers, 1959). Results of the magnetic observations carried out on that occasion are summarized below:

Tristan da Cunha (37°03′ S., 12°18′ W.)
1958 April 29

Station	Magnetic Declination	Horizontal Intensity γ	Vertical Intensity γ
A	−28° 05′.0	15832	−22524
B	−28° 10′.4	15846	−22819

Gough Island (40°20′ S., 9°55′ W.)
1958 May 1

| Station	Magnetic Declination	Horizontal Intensity (γ)	Vertical Intensity (γ)
A	−25° 03′.6	18059	—
B	—	—	−21768
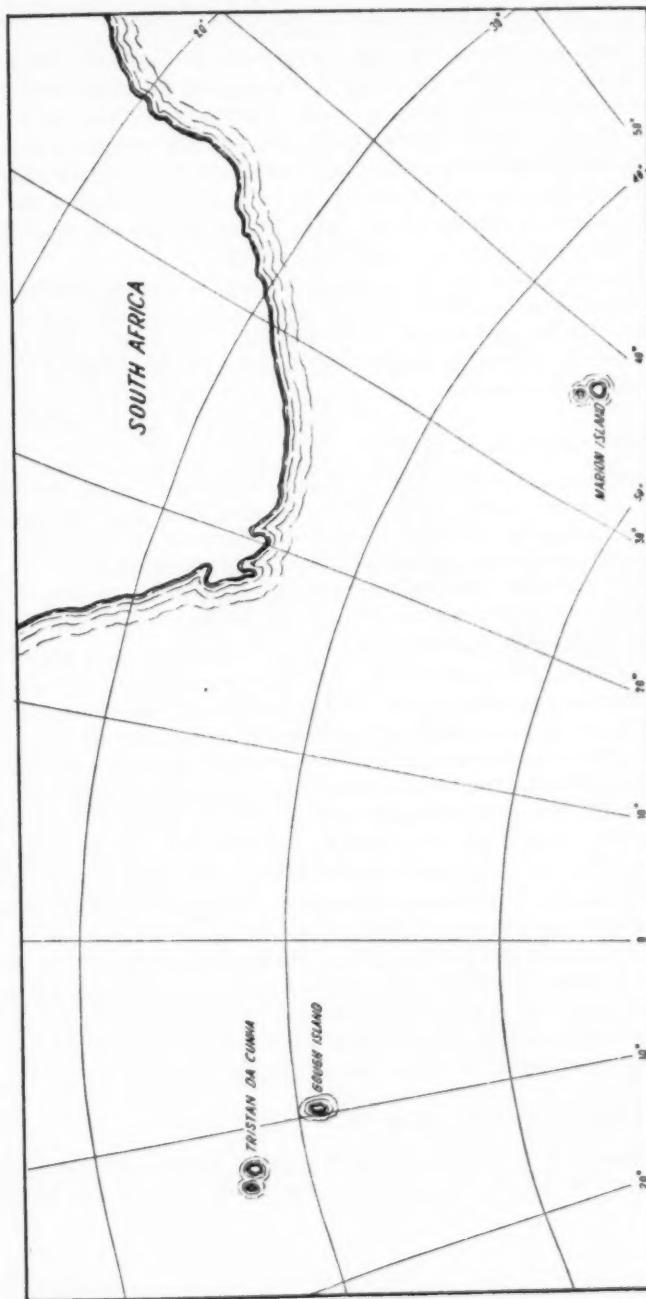
FIG. 1. Map showing geographical position of the islands.

III. MARION, TRISTAN AND GOUGH, 1960

During February–March 1960, the Department of Transport chartered the British ship R.S.S. *Shackleton* to carry out relief voyages to the island meteorological stations. Arrangements having been made for a geophysicist from the Geological Survey (one of us, B.L.W.) to accompany the ship on these voyages, it was decided by the Director of Geological Survey, in consultation with the Chief of the Hermanus Magnetic Observatory (co-author of this paper, A.v.W.) to extend the secular variation programme to Marion Island, and to arrange for the reoccupation of the stations previously established on Tristan and Gough.

The instruments used for the magnetic observations were supplied by and calibrated at the Hermanus Observatory. They were (*a*) a Quartz Horizontal-force Magnetometer (QHM.455) for the determination of magnetic declination and horizontal intensity, and (*b*) a Magnetometric Zero Balance (BMZ.216) for the vertical intensity measurements.

MARION ISLAND (46°51′ S., 37°52′ E.)

Some difficulty was experienced in finding a suitable site for the magnetic stations. On the lower reaches of the island, the damp bog and moss-covered soil offered a poor footing for the instruments. After a thorough reconnaissance of the area in the vicinity of the meteorological station a site was selected on a rise approximately 740 feet due south of Marion House (fig. 2). The two stations, A and B, are 48 feet apart and are marked by $2'' \times 3''$ wooden piles driven into the ground so as to protrude about two feet above the surface. While at station A the pile struck solid rock at a depth of about four feet, the pile at station B continued down for almost six feet without encountering any solid formation. Although the stakes marking the two stations are of special damp-resistant wood, it is recommended that they be replaced with either aluminium or brass piles when next these stations are reoccupied.

Due to the inclement weather, the magnetic programme on the first day, March 7, was limited to a few preliminary observations with the BMZ. On the following day the weather, though still unfavourable, permitted an almost uninterrupted series of observations from 0320 until 1519 hours U.T. The readings were, however, considerably hampered by vibration and constant changes of level in the observing instruments due to the insecure footing provided by the soft, damp soil.

The reference mark used for determining the magnetic declination at station A is the thicker (and more westerly) of two 4-foot posts standing about 250 feet east of the theodolite hut. The true bearing of this mark as determined by the personnel of the meteorological station on the island, is $6°2$ west of true north, or $-6°2$ if reckoned from north round by east in the usual way.

TRISTAN DA CUNHA (37°03′ S., 12°18′ W.)

The location of the stations previously established on this island (see Section II above) is clearly shown on the accompanying sketch (fig. 3) and photograph (Plate Ib).
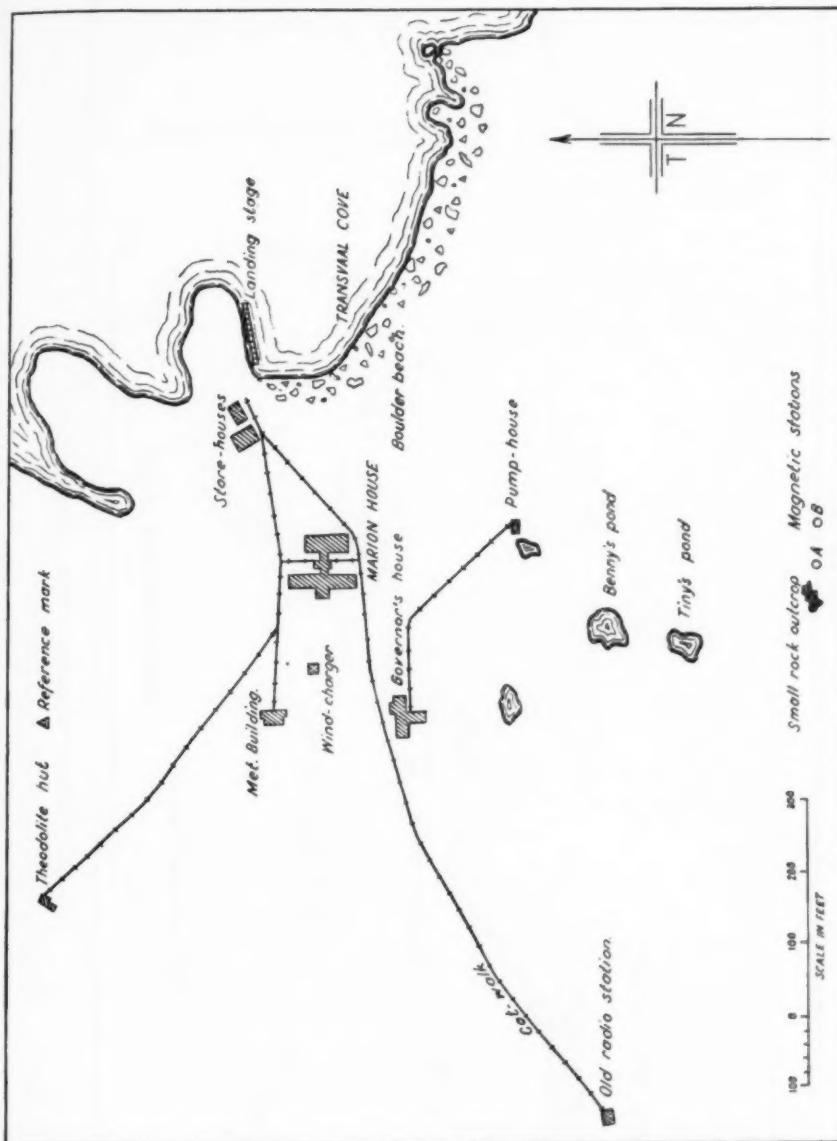
FIG. 2. Location of magnetic stations, Marion Island.
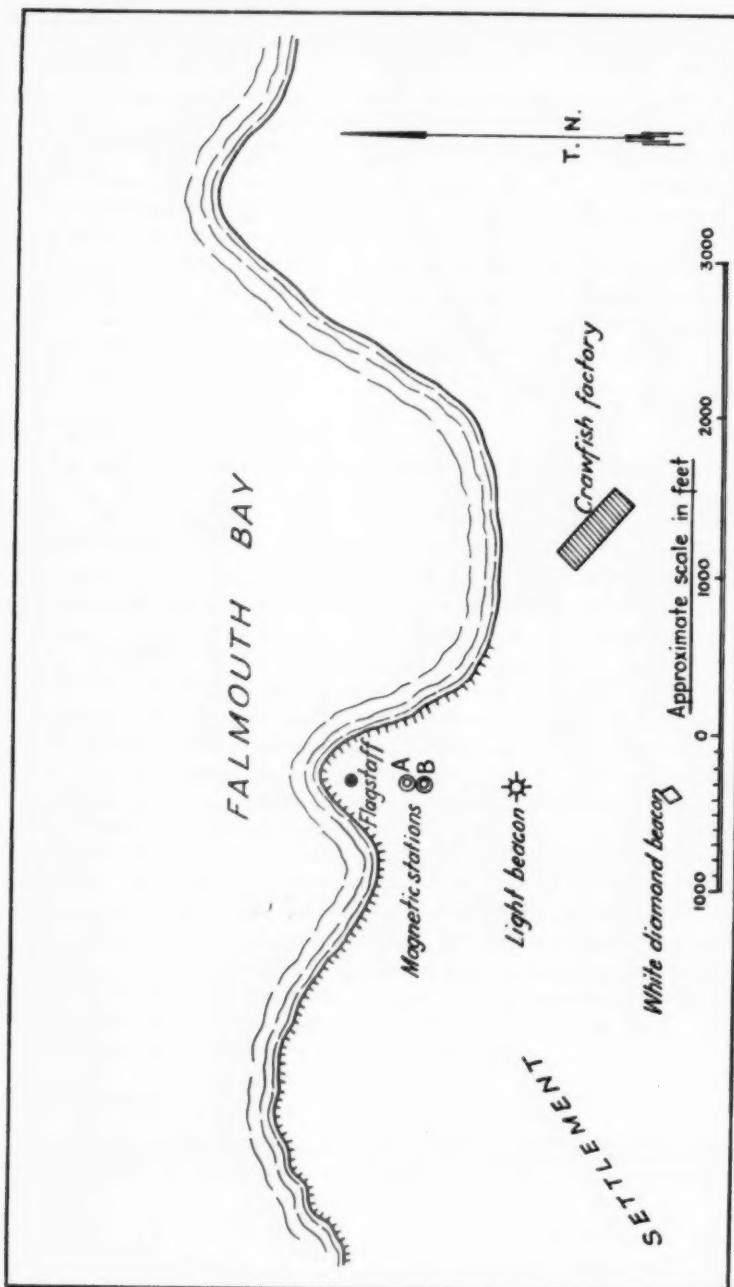
FIG. 3. Location of magnetic stations, Tristan da Cunha.
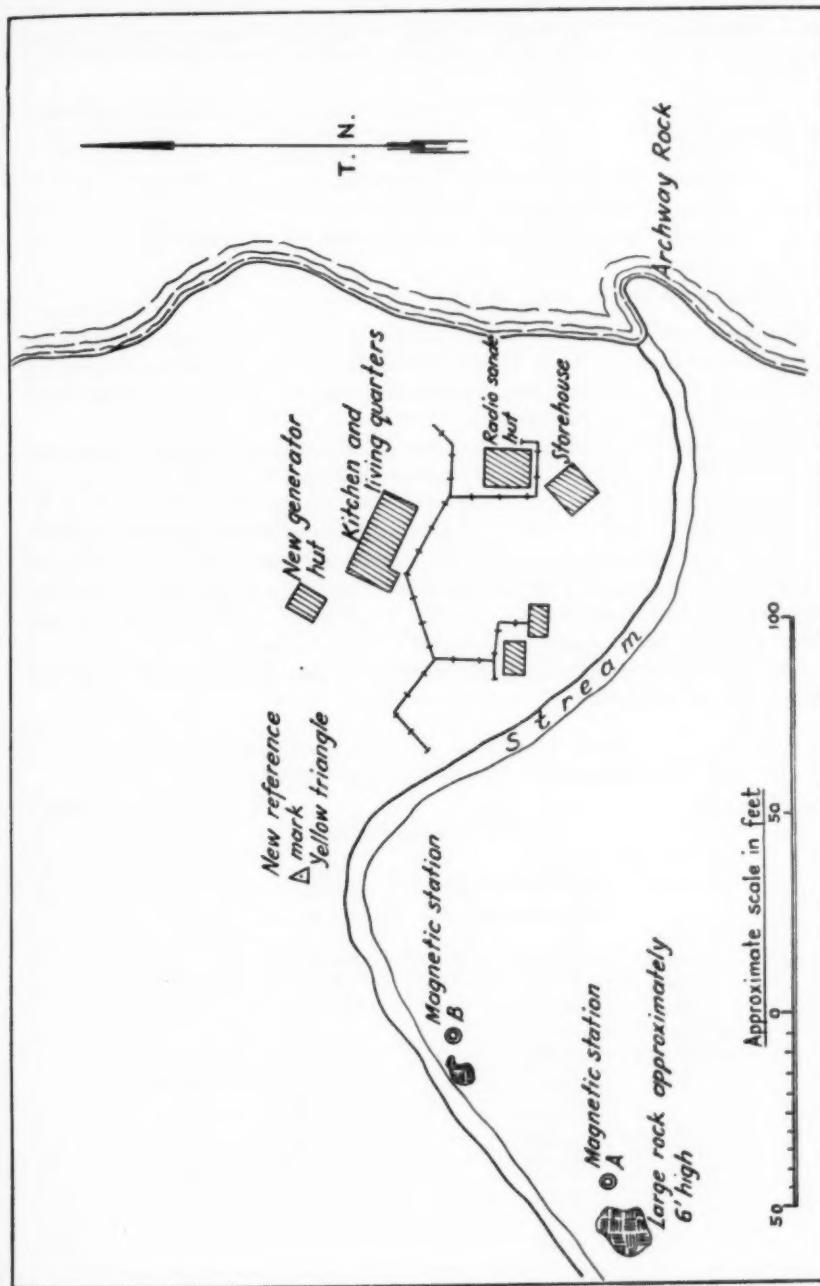
Fig. 4. Location of magnetic stations, Gough Island.

A complete series of observations was carried out at both stations from 1400 hours to 1800 hours U.T. on March 21, 1960. As the ship was due to sail for Gough Island on the following day, the magnetic programme on March 22 was limited to a few readings at each station.

In determining the magnetic declination, the same reference marks and azimuths were used as in 1958:

Station A to Triangular White Beacon .. .. 78°45′.2
Station B to Triangular White Beacon .. .. 77°57′.0
Transit Line to Diamond White Beacon.. .. 174°07′.3

GOUGH ISLAND (40°20′ S., 9°55′ W.)

The stations on Gough Island are situated on the bank of a stream flowing down the glen towards Archway Rock (fig. 4). Some difficulty was experienced in locating the station marks as both had been covered with soil and debris during the floods recently experienced on the island.

As the elevations of both the previous azimuth marks, Archway Rock and Hag's Tooth, were beyond the vertical reach of the QHM telescope, a new reference mark was established at about the same level as the instruments when set up at the stations. The new point is marked by a 12-inch equilateral triangle painted in yellow on the rock face immediately north of the stream and practically in line with the two stations. The larger of the two holes chiselled in the rock near the centre of the triangle was selected as reference mark. The value 40°.46 obtained for the bearing of this mark from station A should be regarded as provisional.

A complete programme of magnetic observations was carried out at both stations on March 24 and 25, 1960.

IV. RESULTS OF MAGNETIC OBSERVATIONS, 1960

MARION ISLAND

MAGNETIC DECLINATION (D)

$$D = C - M$$

where M is the magnetic azimuth and C the true azimuth of the reference mark.

Date	Period (U.T.)	Number of Observations	Magnetic Declination	Final Mean
8/3/60	0320–0332	3	C − 22° 12′.3	
(Station A)	0400–0412	3	11·5	
	0027–0639	3	12·3	Station A:
	0706–0718	3	09·8	C − 22° 06′.8
	1141–1154	3	02·3	
	1210–1222	3	00·3	
	1456–1508	3	C − 21° 59·2	

HORIZONTAL INTENSITY

Date	Period (U.T.)	Number of Observations	Horizontal Intensity	Final Mean
8/3/60	0323–0330	2	14714 γ	
(Station A)	0403–0410	2	14711	
	0631–0637	2	14690	Station A:
	0709–0717	2	14680	14679 γ
	1144–1152	2	14646	
	1214–1220	2	14653	
	1459–1506	2	14658	
8/3/60	0452–0455	1	15206	Station B:
(Station B)	0551–0600	2	15197	15201

VERTICAL INTENSITY

Date	Period (U.T.)	Number of Observations	Vertical Intensity	Final Mean
7/3/60	0826–0829	2	−31832 γ	Station B:
(Station B)	0841–0844	2	−31832	−31832 γ
8/3/60	0613–0617	2	−32188	Station A:
(Station A)				−32188
8/3/60	0348–0353	2	−31847	
(Station B)	0431–0436	2	42	
	0652–0659	2	49	Station B:
	1201–1205	2	26	−31837
	1228–1232	2	24	
	1514–1519	2	32	

Note: Height of instrument, h = 3′ 10″ ± 1″ (see section I above).

TRISTAN DA CUNHA

MAGNETIC DECLINATION

Date	Period (U.T.)	Number of Observations	Magnetic Declination	Final Mean
21/3/60	1410–1420	3	−27° 58.2	
(Station A)	1440–1451	3	56.2	
	1522–1532	3	52.7	Station A:
	1611–1622	3	52.2	−27° 54.6
	1824–1835	3	53.7	
21/3/60	1639–1651	3	−27° 53.8	Station B:
(Station B)	1720–1734	3	53.7	−27° 53.7
	1756–1808	3	53.5	
22/3/60	0927–0936	3	−28° 01.5	Station A:
(Station A)				−28° 01.5

HORIZONTAL INTENSITY

Date	Period (U.T.)	Number of Observations	Horizontal Intensity	Final Mean
21/3/60	1413–1419	2	15696 γ	
(Station A)	1443–1449	2	15700	
	1524–1530	2	15704	Station A:
	1614–1620	2	15714	15704 γ
	1827–1834	2	15704	
21/3/60	1642–1650	2	15653	Station B:
(Station B)	1723–1730	2	15648	15648
	1759–1805	2	15642	
22/3/60	0929–0934	2	15721	Station A:
(Station A)				15721

VERTICAL INTENSITY

Date	Period (U.T.)	Number of Observations	Vertical Intensity	Final Mean
21/3/60	1632–1634	1	−22511 γ	Station A:
(Station A)	1713–1715	1	511	−22516 γ
	1751–1753	1	526	
21/3/60	1404–1406	1	−22750	
(Station B)	1433–1437	2	72	Station B:
	1518–1519	1	77	−22771
	1608–1609	1	80	
	1820–1822	1	78	
22/3/60	0924–0925	1	−22784	Station B:
(Station B)	0942–0944	1	82	−22783

Note: Height of instrument, Station A: h = 4′ 2″ ± 1″.
Station B: h = 4′ 0″ ± 1″.

GOUGH

MAGNETIC DECLINATION (D)

$$D = C - M$$

where M is the magnetic azimuth and C the true azimuth of the reference mark.

Date	Period (U.T.)	Number of Observations	Magnetic Declination	Final Mean
24/3/60	0935–0945	3	C_1 −65° 30′.5	
(Station A)	1026–1036	3	30·4	
	1217–1227	3	26·6	Station A:
	1449–1458	3	18·5	C_1 −65° 23′.5
	1515–1525	3	15·9	
	1705–1716	3	19·3	
25/3/60	0958–1008	3	C_1 −65° 31′.7	Station A:
(Station A)	1346–1356	3	19·9	C_1 −65° 25′.8
25/3/60	1030–1042	3	C_2 −69° 47′.5	Station B:
(Station B)	1324–1333	3	37·2	C_2 −69° 42′.4

2

HORIZONTAL INTENSITY

Date	Period (U.T.)	Number of Observations	Horizontal Intensity	Final Mean
24/3/60	0938–0944	2	17912 γ	
(Station A)	1028–1034	2	905	
	1220–1225	2	17892	Station A:
	1451–1457	2	908	17901 γ
	1516–1523	2	904	
	1708–1714	2	886	
25/3/60	0959–1006	2	17093	Station A:
(Station A)	1348–1354	2	17870	17886
25/3/60	1033–1040	2	18106	Station B:
(Station B)	1326–1332	2	18086	18096

VERTICAL INTENSITY

Date	Period (U.T.)	Number of Observations	Vertical Intensity	Final Mean
24/3/60	0931–0951	2	−21743 γ	
(Station B)	1023–1040	2	44	
	1214–1232	2	44	Station B:
	1446–1529	3	34	−21740 γ
	1703–1717	2	37	
25/3/60	0954–1013	2	−21747	Station B:
(Station B)	1342–1359	2	47	−21747
25/3/60	1026–1046	2	−20988	Station A:
(Station A)	1322–1336	2	84	−20986

Note: Height of instrument, Station A: = 3′ 11″ ± 1″.
Station B: = 3′ 9″ ± 1″.

V. CONCLUSION

As mean values obtained from a one-day set of observations are liable to be affected by diurnal changes and by the day-to-day variability of the magnetic elements, it is too early yet to make any inferences regarding the secular variation at Tristan da Cunha and Gough Island. It is recommended that the magnetic stations on the islands be reoccupied at intervals of about five years.

REFERENCES

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Plate I

a. Marion Island

b. Tristan da Cunha

c. Gough Island